UNIVERSITY OF ALBERTA

The Parasites of Pacific Halibut, *Hippoglossus stenolepis*, in the Northeastern Pacific: Ecological Patterns in Time and Space.

by

Reginald Brent Blaylock

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Doctor of Philosophy

Department of Biological Sciences

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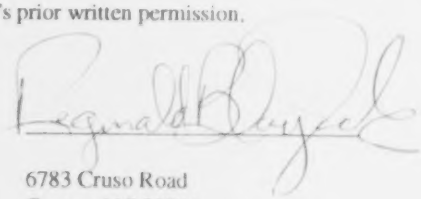

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **THE PARASITES OF PACIFIC HALIBUT, *HIPPOGLOSSUS STENOLEPIS*, IN THE NORTHEASTERN PACIFIC: ECOLOGICAL PATTERNS IN TIME AND SPACE** by **REGINALD BRENT BLAYLOCK** in partial fulfilment of the requirements for the degree of **DOCTOR OF PHILOSOPHY.**

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DEDICATION

To my parents, Frank and Ramona Blaylock, without whose love and support completion of this thesis would not have been possible. Indeed, their attitude of allowing me the freedom to pursue my dreams, while possibly frustrating for them, has been an example and an inspiration. I also wish to acknowledge my grandparents who loved and supported me as well. I wish all of them had lived to see this day.

ABSTRACT

The ecology of the parasites of Pacific halibut, *Hippoglossus stenolepis*, was studied through various spatial and temporal scales using data from 536 fish collected from northern California to the northern Bering Sea. Fifty-nine parasite taxa were identified from three size-classes (104 recruits [<10 cm], 104 juveniles [10-55 cm], 328 subadults/adults [>55 cm]). Halibut harbor among the richer and more abundant parasite communities found in marine fishes due to the interplay of host size, diet, mobility, gregariousness, and lifespan. The parasites are largely ecological generalists found in a wide variety of marine fishes. However, the parasite community in halibut is more similar to those in other flatfishes than to those in ecological analogs.

Recruits harbor few parasites, but parasite species and individuals accumulate rapidly with age and length and reflect the shift from a crustacean to a fish diet. Growth rate appears to determine the number of parasite individuals in a given fish, reflecting food intake, but the number of species plateaus by age six. The smallest fish in the 5, 6, and 7 year age-classes have more parasite individuals than slightly larger fish in the same age class and weigh less than expected for their size; they appear to be debilitated by parasites.

The parasite fauna shows three zoogeographic zones in the northeast Pacific, with boundaries near the southern Queen Charlotte Islands and in the vicinity of Kodiak Island. "Fuzziness" around these boundaries is probably due to small-scale fish movement. These boundaries roughly correspond to those previously established in free-living fauna.

Based on numbers of individuals of eight species of long-lived juvenile parasites, Pacific halibut can be divided into two stocks: a southern stock which ranges from California to the southern Queen Charlotte Islands and a northern stock from west and north of the southern Queen Charlotte Islands. Bering Sea fish form a subpopulation of the northern stock.

Comparison of community patterns at different spatial scales suggests that the patterns in the parasite community of halibut are created largely by variation among individual fish taken at the same time and place, but that scales ranging from zoogeographic to local levels also contribute significantly.

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CHAPTER 1 - GENERAL INTRODUCTION

Community ecology involves the elucidation of patterns in the assemblages of organisms, evaluation of the predictability of those patterns, and determination of the processes responsible for the observed patterns. Current concerns include examining the extent to which communities exhibit discernable, predictable structure and whether observed patterns reflect historical or ecological influences (or a combination of both). Of potentially more importance is the realization that patterns are dependent upon the scale of the observation. Even though Hutchinson (1953) recognized early on that pattern is related to scale, many ecological studies have focused either on identifying patterns or examining processes at a single scale. Recently, however, there has been an upsurge in concern for framing conclusions in the context of scale. Dayton and Tegner (1984), Bush and Holmes (1986), Wiens (1986), and Addicott et al. (1987) (among others) note that patterns at different scales are produced by different processes, ranging from zoogeographic processes operating at the largest scale to interactions in patchy local conditions operating at the smallest scale. Levin (1992) argued that it is critical to realize that different processes are important at different scales and to integrate the interplay of these processes in order to fully understand the relative importance of mechanisms. Holmes (1990) and Tonn (1990) perceived this interplay of processes as a series of screens or filters through which the components of a fauna must pass to produce the observed pattern.

These filters may exist at several spatial scales because parasites infect individual hosts that form local populations, which are parts of both local and regional host communities. Further, hosts, both as individuals and as species, exist through ontogenies and time, providing various temporal scales. The actual parasite community in an individual host, therefore, can be regarded as the product not only of processes (screens) operating at or within the individual host level, but also of the screens operating at each successively higher scale (spatial or temporal) that limit or modify the potential fauna available at the lower scales.

In this thesis I will examine the patterns of parasitism in Pacific halibut at spatial scales including within individual hosts, fish taken in the same haul, composites of hauls from the same general area (localities), and zoogeographic regions. I will also examine one temporal scale, that associated with the ontogeny of Pacific halibut.

Parasites and ecology

Although parasites have been of general interest for centuries, the ecology of parasites has been explicitly recognized as a coherent discipline only in the 20th century. The Russian academician V.A. Dogiel is largely credited with establishing the field. He and his co-workers recognized the importance of examining the relationships among the host, the parasite, and the environment and were committed to the idea of a vibrant system that determines how and where parasites assort themselves among hosts. The publication of the English editions of Dogiel et al.'s *Parasitology of Fishes* (1961) and Dogiel's *General Parasitology* (1964) represents the summation of the classic tenets from which the field has evolved.

Holmes (1961, 1962) added another dimension to the field by quantitatively demonstrating that parasites interact with one another within a host. As a result of these publications, parasitologists became more ecologically minded. Esch et al. (1975) framed parasitological issues in a distinctly ecological context. Their publication formalized the now implicit hierarchical view of parasite populations. Holmes and Price (1986) expanded the concept to the community level. Infracommunities are all the parasites in a single host. Component communities represent the infracommunities within a host population. Compound communities are all the parasites in an ecosystem. Price (1980) and Holmes and Price (1986) began viewing hosts as resource patches that were organized in a similar hierarchical fashion.

At the individual host (infracommunity) level, hosts provide discrete, isolated parasite communities with clear boundaries within which the parasites select specific habitats and reproduce, and within which any direct interactions between parasites, or between parasites and their host, must occur. The primary historical factor active at this level is host specificity; the primary ecological factors are transmission rates, host immune or avoidance responses, and interactions between parasites. If transmission rates are adequate, a predictable, fairly stable pattern may emerge, with a group of parasite species regularly associated with most individuals of a given host species (Holmes 1990). Such "core species" (Hanski 1982) are usually both regionally common (present in a high proportion of hosts) and locally numerous in most host individuals. Regular cooccurrence and numerical dominance of a suite of core species should give the community discernable structure and provide opportunities for parasites to interact. Holmes and Price (1986) characterized such a packed, species-rich community as interactive.

If, on the other hand, transmission rates are low, and particularly if host specificity is unimportant, chance exposure to infective stages is likely to predominate, and communities are unlikely to show predictable structure. Core species would be few or absent, generalist species (those found in a wide variety of hosts) would be likely to dominate, and the composition of the parasite community would be essentially stochastic (Holmes 1990). This type of chance assemblage characteristically has few species, much empty space, and little opportunity for interaction between parasites. Holmes and Price (1986) classified this type of community as isolationist.

At the host population (component community) level, transmission rates, or the ability of the host to maintain parasites, may be affected by factors correlated with host sex, age, size, or food habits. Because individual hosts provide replicates of parasite communities, the effects of these factors may be easily assessed. The kinds and numbers of parasites available to be sampled by members of the local population depend not only on the size of that local population, but also on the mix of other potential definitive and intermediate hosts, and their parasites, available in the local host community. Different localities, although they appear similar, may provide substantially different conditions. Oceanic current regimes may vary locally, resulting in temperature and productivity differences that affect the composition of the local host community. That composition also may depend on the amount of suitable habitat available, the distance from other patches of suitable habitat, or recent historical events (Dayton and Tegner 1984).

At the regional scale, both parasite and host communities are determined largely by zoogeography. Different regions may provide different habitats, and large scale current patterns may serve as barriers to dispersal between surrounding regions. Climatic differences also may differentiate regions. These factors may determine patterns of host or parasite distribution, especially in freshwater situations, where migrations between habitat patches are more constrained (Tonn 1990).

Fishes, Parasites, and Ecology

Fish parasite communities are expected to be depauperate, stochastic, and transmission-driven with little opportunity or necessity for interactions (compared to birds and mammals) due to the lesser requirements of ectothermy, the lesser complexity of the gastrointestinal tract, lower vagility, and narrower diets (Kennedy et

al. 1986a). These predictions largely have been upheld (Kennedy and Bakke 1989; Kennedy 1990; Aho et al. 1991; Janovy et al. 1991; McDowell et al. 1992; Kennedy 1993), but there is an increasing appreciation of exceptions to the general rule (see Sousa 1994). The majority of work has been in freshwater systems. Fewer studies have examined parasite community dynamics in marine systems (but see George-Nascimento 1987; George-Nascimento and Iriarte 1989; Thoney 1991; Belghyti et al. 1994). Most studies provide general support for Kennedy et al's. (1986a) predictions, but Holmes (1990) suggests that communities of marine fish parasites have about the same number of individuals, but more species than those in freshwater fishes (but see Cislo and Caira 1993; Poulin 1995). These differences have been attributed, in part, to the greater vagility and broader diets of marine fishes compared to freshwater fishes.

Analyses of fish parasite communities (indeed of most parasite communities) have generally looked at single scale patterns. Larger scale processes such as the effect of lake trophic status (Wisniewski 1958), the effect of predator-prey relationships (Esch 1971), historical factors (Kennedy 1978), or locality (Kennedy et al. 1986b) have been investigated. In marine fishes, there have been various observations on zoogeography since the 1940's (reviewed by Rohde (1993)), but the data are too scarce to allow wide-ranging conclusions. A substantial body of work uses large scale parasite phenomena to distinguish between stocks of some commercially important fishes (see Margolis 1982; Kabata et al. 1988; Williams et al. 1992) or to identify relationships between parasite community composition and environmental or dietary factors (reviewed by Rohde 1993; Campbell 1983; Poulin 1995, 1996). At the infracommunity level, few appropriate analyses have been attempted, especially in marine fishes. Site preferences have been noted (Uglem and Beck 1972; Kennedy 1985; Janovy et al. 1991 for freshwater fishes and Kabata 1959; MacKenzie and Gibson 1970; Buchmann 1991; Holmes and Bartoli 1993 for marine fishes), but they may be caused by a variety of physical, historical, or ecological processes. With respect to ecological processes, Grey and Hayunga (1980) report competition between cestodes and acanthocephalans in white sucker (*Catostomus commersoni*) and Bates and Kennedy (1990) report competition among acanthocephalans in rainbow trout. For marine fishes, Sogandares-Bernal (1959), MacKenzie and Gibson (1970), Rohde (1979), and Bartoli (1990) hypothesize some degree of interactive site segregation either for reproductive purposes or as a result of competition. But, as Holmes and Bartoli (1993) point out, these analyses were performed on data summed across all hosts in a sample, which

may obscure true patterns. As a result, the importance (either relative or absolute) of infracommunity processes is largely unknown. More importantly, as Kennedy and Bush (1994) point out, few parasite studies have looked explicitly at the relationship between patterns and the scales at which they occur.

Parasites and Fisheries Science

Fisheries management is dependent on estimating the minimum numbers of spawning adults required to maintain a population (stock) at a specified level and adjusting harvest rates accordingly. If one assumes a homogeneous population, this process is fairly simple; however, many marine fish "populations" are composed of individuals from several discrete stocks. An ability to distinguish these stocks is crucial for maintaining the "population" and the continued existence of different stocks. In addition, information on the various factors that may influence the condition of the stocks is necessary.

Parasites have been used successfully in fisheries management. Implicit in this use are the ecological patterns at the various spatial or temporal scales. Because different biotic and abiotic processes operating in different areas may produce different parasite assemblages, ecological patterns in parasite assemblages may be used to distinguish stocks. Margolis (1963) was one of the first to use this technique to distinguish between Asian and North American sockeye salmon (*Oncorhynchus nerka*) based on the presence of certain parasites in either western Alaska or Kamchatka and their absence in the other region. Since then, several authors have used the presence/absence model to delineate stocks of a number of species including flounder (*Platichthys flesus*) (Gibson 1972) and sablefish (*Anoplopoma fimbria*) (Kabata et al. 1988). Leaman and Kabata (1987) and Aldana et al. (1995) expanded the technique to consider the population structure of parasites of different stocks of fishes. Arthur and Arai (1980), Bailey et al. (1988), Arthur and Albert (1993), and Speare (1995) used parasite community patterns to distinguish stocks or determine stock composition of a "population".

Temporal parasite patterns also have been used as indicators of host biology. Marine fishes often undergo compensatory migrations from nursery areas or seasonal/reproductive migrations. Because juvenile fish may eat different organisms and because different areas may have different parasite pools, parasite assemblages in a host may change over time. MacKenzie (1985) and McGladdery and Burt (1985) used

parasites to trace recruitment migrations and spawning behavior of herring (*Clupea harengus*) in the North Sea and northwest Atlantic, respectively. Bray and MacKenzie (1990) elucidated seasonal migrations of herring in the North Sea. Over a larger time scale, parasites may provide evidence on the interrelationships among, or the phylogeny of, the hosts. Brooks et al. (1981), for example, used parasites to conclude that South American freshwater potamotrygonid rays living in Atlantic drainages originated in the Pacific rather than the Atlantic.

Parasites may also affect fish condition. Rohde (1993) noted that parasites may directly kill or affect reproduction, reduce fish condition, or make marketing more difficult and expensive. Most known direct kills are coupled with altered environmental conditions (see Rohde 1993; Blaylock and Margolis 1996). Kabata (1958) showed that the number of copepods affected the condition of haddock (*Melanogrammus aeglefinus*). Boyce (1979) demonstrated that a tapeworm reduces the growth and vitality of sockeye salmon fry. Johnson et al. (1996) suggested that a parasitic copepod affects the number of sockeye salmon surviving to spawn.

Some parasites also may have a negative impact on the marketing of fish. Myxosporea such as *Unicapsula*, *Kudoa*, and *Henneguya* cause flesh quality problems that affect the value and desirability of the fish (Rohde 1993; Kent et al. 1994). *Unicapsula* fills and distorts muscle fibers so that they appear wormlike (Davis 1923). *Kudoa* and *Henneguya* cause pseudocysts and soft flesh (Kent et al. 1994). Reliable estimates on the economic impact of these myxosporeans are not available, but, particularly in salmonid aquaculture, there is enough concern to warrant funding of several studies on *Kudoa* (personal observation).

Helminths relevant to the marketing of marine fish include primarily the larval anisakid nematodes (primarily *Anisakis simplex* and *Pseudoterranova decipiens*) which are among the most common parasites of marine fish (Rohde 1993), but may also include plerocercoids of *Diphyllobothrium* sp. and other cestodes. These worms form visible cysts in muscle tissue that affect the appearance of the product. In addition, some are infective to humans who eat raw, undercooked, or improperly frozen fish, and thus are of public health concern. *Anisakis* is of particular concern because of the larvae's ability to penetrate the gastrointestinal tract and cause an intense inflammatory response that often requires surgical removal of the worm (Sakanari and McKerrow 1989).

The system

Pacific halibut are large flatfish on the continental shelf of the North Pacific Ocean ranging from southern California to northern Japan (Hart 1973; NOAA 1990). They are demersal, generally inhabiting depths of 500 meters or less, although they do move to deeper waters during the winter spawning season and shallower waters during the summer feeding season (IPHC 1986; NOAA 1990). Eggs are spawned in winter and hatch as they rise to the surface, where prevailing currents tend to pool the larvae (IPHC 1986). In about two months larvae begin feeding on plankton and by six months they have completed transformation and settled in shallow inshore areas, where they spend 1-3 years feeding primarily on crustaceans. Four- to seven-year olds move to deeper water, become progressively more piscivorous, and begin a compensatory migration to counterbalance egg drift. Adults, which are less extensively migratory (Skud 1977), are largely piscivorous, but are opportunistic feeders throughout the water column (IPHC 1986; Best and St-Pierre 1986). Halibut are sexually dimorphic. Males grow slowly, generally mature by age eight, and reach a maximum of 1.5 meters and live up to 27 years. Females grow faster, but do not mature until age 12-13, and may reach nearly 3 meters and live more than 40 years (IPHC 1986; NOAA 1990). Halibut in the commercial fishery average 14-18kg and one to two meters in length (IPHC 1986).

Halibut support one of the top 5 commercial fisheries in North America (IPHC 1986) and are a prized sport fish. These fisheries annually inject well over $100 million (US) into west coast economies (NOAA 1990). As a result of this commercial importance, careful management of the resource is necessary. Parasites may provide information useful in several aspects of management. Identification of zoogeographic differences in parasites may aid in determining stock boundaries or the extent of migrations. Variation in parasites due to host age, sex, or size may provide information on the ecological relationships throughout the ontogeny of halibut. In addition, identification and evaluation of possible halibut or human pathogens is useful.

Previous work on parasites of halibut is limited. Mamaev et al. (1963) recorded 27 helminth species (15 digeneans, 6 cestodes, 4 nematodes, and 2 acanthocephalans) from halibut in the western Pacific. Margolis and Arthur (1979), Love and Moser (1983) and McDonald and Margolis (1995) report 2 myxosporeans, 3 monogeneans, 12 digeneans, 2 cestodes, 4 nematodes, 3 acanthocephalans, 2 leeches, 6 copepods, and 1

isopod from the eastern Pacific. However, these observations are largely incidental. There has been no comprehensive study of the parasites of halibut in the eastern Pacific.

Objectives

This study was designed:

1) to survey the parasites of Pacific halibut,

2) to determine whether or not there are patterns in the parasite communities of Pacific halibut at different ecological scales,

3) if so, to assess the relative importance of processes operating at each of those scales to produce the observed patterns, and

4) to assess the significance of protozoan and metazoan parasites of Pacific halibut for management of the resource.

In Chapter 2, I present the basic survey data and examine host level influences such as those of sex, age, and size on the parasite community. I also examine the importance of host specificity and evidence on possible effects parasites have on the host. In Chapter 3, I examine zoogeographic zonation in the parasites of Pacific halibut and compare it to zonation in free-living organisms. In Chapter 4, I use parasites to discriminate stocks of halibut. In Chapter 5, I compare community patterns at various spatial scales. In Chapter 6, I summarize the study and review the extent to which the objectives have been met.

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CHAPTER 2 - HOST-LEVEL INFLUENCES

Polyanski (1961) concluded that five host-level factors - diet, lifespan, mobility, gregariousness and size - were the primary determinants of the composition and abundance of the parasite fauna of marine fishes. Generally, larger, more mobile and gregarious hosts, and those that eat a wider variety of foods, have more parasites. He also noted the interplay of host age with these factors, and gave examples of how the parasite fauna of several fishes change with age. Pacific halibut are among the largest fish in the ocean (maximum size 3 meters and 300 kg), they undergo extensive migrations, and are opportunistic feeders. In addition, they can live more than 40 years, during which time they undergo major ontogenetic niche shifts. Halibut do not school, but neither are they territorial. Halibut, therefore, meet almost all of Polyanski's criteria for a rich and abundant parasite fauna. Many studies (e.g., George-Nascimento 1987, Thoney 1991, Belghyti et al. 1994) have confirmed the significance of host size and/or diet, but few have examined potential interactions among the factors or examined patterns over the ontogeny of a single host species.

Host-level factors may also include phylogenetic patterns. Ecologists have often debated the relative importance of ecology and phylogeny in producing community patterns. Holmes (1990) suggested that common, related fishes in the same community may share more parasites relative to other fishes. Poulin (1995) found that controlling for host phylogeny eliminated the effects of most ecological factors in determining the richness of parasite communities. Indeed, it is reasonable to conclude that evolutionary history may predispose a host for certain types of parasites that its ancestor may have possessed. However, the question of whether ecological changes among related hosts overrides patterns associated with phylogeny is unresolved. Therefore, should halibut share more parasites with other flatfishes or, alternatively, with other fishes with similar ecological niches?

One host-level factor, condition, may be affected by parasites. Kabata (1958) found that the condition of haddock (*Melanogrammus aeglefinus*) was related to the number of copepods. Boyce (1979) showed that the tapeworm *Eubothrium salvelini* reduced the growth and vitality of sockeye salmon (*Oncorhynchus nerka*) smolts. Adlard and Lester (1994) showed that a parasitic isopod significantly depressed growth, reproduction,

and survivorship of the coral reef fish *Chromis nitida*. No study of parasites in relation to condition of halibut has been done.

In this chapter, I:

1) present the results of a survey of the parasite fauna of three size-classes of Pacific halibut from northern California to the Bering Sea,

2) describe changes in the parasite fauna through the size-classes of halibut,

3) analyze the effects of host size, sex, and age on the parasite fauna of Pacific halibut in the eastern North Pacific,

4) examine the relationship between the parasite fauna and fish condition, and

5) compare the parasite fauna of Pacific halibut to those of other marine fishes.

MATERIALS AND METHODS

A total of 536 fish was examined. Fish were caught by staffs of the International Pacific Halibut Commission (IPHC) and the U.S. National Marine Fisheries Service during the summers of 1990-1992 (using longlines and trawls). Samples were bagged individually and immediately deep frozen at sea for later examination. Of the 536 fish, 104 were recruits (<10 cm) from the vicinity of Kodiak Island, Alaska, 104 were juveniles (10-55 cm) from 5 localities from the Queen Charlotte Islands, British Columbia, to the Bering Sea, and 328 were subadults/adults (hereafter referred to as adults) (>55 cm) from 15 localities from northern California to the Bering Sea.

In the laboratory, fish were weighed and measured (fork length). Otoliths were collected and used to determine ages by the aging laboratory of the IPHC. Standard parasitological techniques were used for examination. Fish were thawed, the external surface was rinsed, the rinse was filtered through a fine mesh screen, and the screen was examined under a dissecting microscope for ectoparasites. Fins and eyes were removed, teased apart, and examined under the dissecting microscope. The gill arches were removed and examined individually, including opening the main blood vessels within the gills. The heart, liver, spleen, gonads, and kidney were removed, examined for encapsulated parasites on the exterior, and squashed between plexiglass plates for further examination over a light source. Gonads were examined to determine sex, liver weights were taken as an index of condition, and gonad weights and descriptions were taken as a measure of maturity. The gall bladder and urinary bladder were opened longitudinally and examined for macroparasites with a dissecting scope. The digestive tract was removed and divided into 15 sections (stomach, 4 pyloric ceca, and 10 intestinal sections), each of which was opened longitudinally, scraped, and washed into separate containers that were examined for helminths under the dissecting scope. Squash preparations were made from liver, spleen, kidney, gonads, intestine, muscle, and scrapings from the internal walls of the gall bladder and urinary bladder and examined under the compound scope at 320-400X for myxosporeans/protozoans. Brain tissue was digested at 37°C in a 0.5% pepsin-hydrochloric acid solution and centrifuged 5 min at 4000 rpm. A squash preparation was then made from a sample drawn from the bottom of the centrifuge tube. Smears were considered negative if parasites were not found within 5 min. The carcass was filleted, and the tissues around the vertebral column were examined for encapsulated parasites. Muscle tissue was divided into 16 sections (7

per side and 2 belly flaps). Belly flaps and 4 sections (2 randomly chosen from each side) were thinly sliced, pressed between plexiglass plates, and examined for encapsulated helminths and myxosporeans over a light source.

Fish in the <10 cm size class were too small for some of these methods. In these fish, the gills, including internal blood vessels and tissues, were examined by pressing between plexiglass plates, the brain was not examined, the digestive tract was examined as a whole, the carcass musculature was examined as a whole, and sex was not determined due to the undifferentiated gonads.

Parasites were tentatively identified (using a dissecting scope or in wet mounts), counted (except for myxosporeans) for each organ or section, cleaned, and fixed in 10% buffered formalin. Myxosporeans were examined and measured as temporary wet mounts before fixation in 10% buffered formalin. Identifications of Monogenea, Digenea, Cestoidea, and Acanthocephala were confirmed after staining in Semichon's acetocarmine and mounting in Canada Balsam. As necessary, nematodes were examined in temporary mounts after clearing in lactophenol or evaporation of glycerine alcohol. As necessary, copepods were dissected and appendages examined. Myxosporeans, recorded as positive/negative, were included in the analyses of numbers of individuals by assigning positives the value of the average number of worms in that fish.

Parasites in the overall sample and in each size class were categorized by prevalence (as defined by Margolis et al. (1982)) into very common, common, and rare species using plots of numbers of species per prevalence category. Division into the categories was based on breakpoints in the respective graphs.

Differences in the halibut parasite assemblage related to host sex, size, age, and condition were initially examined using Mann-Whitney U and Spearman's rank correlations. To account for possible intercorrelations among age, weight, length, and sex, the relationship of sex with parasite number and species number was examined using standard regressions with partial correlations and ANCOVA with each variable as the covariate separately and in concert. Standard regressions, partial correlations using log transformed variables, and residual analyses were used to examine the relationships among parasite number, species number, and condition. Because my primary objective was the identification of heuristic patterns, a significance level of 0.1 was accepted in order to reduce type II error. All procedures were performed in SYSTAT for Windows version 5.05 (Wilkinson et al. 1992).

Comparisons with other marine fishes were made using data presented by Holmes (1990) for gastrointestinal helminths. Data for non-GI helminths, ectoparasites, and myxosporeans were obtained from Arthur and Arai (1980), Arthur (1984), Bourgeois and Ni (1984), Kabata and Whitaker (1984), Scott (1988), and Arthur and Albert (1994). Prevalence and intensity (when available) data from these papers were used to calculate the mean number of species and the mean number of individuals per fish using the methods of Holmes (1990) (Mean number of species = sum of prevalences / 100 and mean number of individuals = $\sum$ (prevalence * sample size * mean intensity) for each species / sample size). When more than one population was sampled, the highest means were used.

The parasite assemblage of Pacific halibut was compared with the parasite assemblages of a selection of other fishes from both the Atlantic and Pacific Oceans using Jaccard's coefficient as the measure of similarity and clustering using average linkage. Data were obtained from Margolis and Arthur (1979), Love and Moser (1983), Arthur and Albert (1994), and McDonald and Margolis (1995). Species included in the analysis and their locations were: Clupeidae: *Clupea pallasi* (Pacific herring - Pacific); Salmonidae: *Oncorhynchus nerka* (sockeye salmon - Pacific), *Oncorhynchus tshawytscha* (chinook salmon - Pacific); Gadidae: *Gadus macrocephalus* (Pacific cod - Pacific), *Gadus morhua* (Atlantic cod - Atlantic), *Melanogrammus aeglefinus* (haddock - Atlantic), *Theragra chalcogramma* (walleye pollock - Pacific); Merluccidae: *Merluccius productus* (Pacific hake - Pacific); Scorpaenidae: *Sebastes alutus* (Pacific ocean perch - Pacific); Anoplopomatidae: *Anoplopoma fimbria* (sablefish - Pacific); Pleuronectidae: *Atherestes stomias* (arrowtooth flounder - Pacific), *Eopsetta jordani* (petrale sole - Pacific), *Hippoglossus hippoglossus* (Atlantic halibut - Atlantic), *Microstomus pacificus* (Dover sole - Pacific), *Platichthys stellatus* (starry flounder - Pacific), *Pleuronectes bilineatus* (rock sole - Pacific), *Pleuronectes vetulus* (English sole - Pacific), and *Reinhardtius hippoglossoides* (Greenland halibut - Atlantic and Pacific).

Voucher specimens are deposited in the Canadian Museum of Nature, Parasite Collection, Ottawa. Representative specimens are also deposited in the University of Alberta Parasite Collection, the parasite collection at the Pacific Biological Station, and in my personal collection.

RESULTS

Fifty-nine taxa of parasites were identified, including 8 Myxosporea (2 of which were *Leptotheca* sp. from the urinary bladder and the gall bladder), 2 Monogenea, 23 Digenea , 4 Cestoidea (2 of which were *Scolex pleuronectis* from the gall bladder and the intestine), 9 Nematoda, 5 Acanthocephala, 7 Crustacea, and at least 1 Hirudinoidea (see Table 2.1). In addition, there were 2 unidentifiable specimens of digeneans, 2 kinds of cestode larvae that were unidentified, but may belong to an identified species, and 1 species of nematode that was unidentifiable.

Fifteen taxa were sufficiently rare (i.e. present in only 1 or 2 fish) to be considered accidental: 7 Digenea (including the 2 unidentifiable taxa), 4 Cestoidea (2 of which were unidentifiable larvae), 3 Crustacea, and 1 Myxosporea.

Parasites were relatively rare in the recruits (mean abundance 0.7 species and 0.5 parasites per fish), but increased rapidly in juveniles (7.1 species and 187 parasites per fish) and adults (11.8 species and 307 parasites per fish). In the juveniles, the mode was 7 species of parasites and 50-100 parasite individuals per fish; in adults, 12 parasite species and 100-200 parasite individuals (Figures 2.1, 2.2). In all cases there was considerable spread around the peak. The distributions, particularly those for numbers of individual parasites, were skewed to the right, suggesting that substantial numbers of fish contain considerably more than the modal numbers. Variance to mean ratios confirmed substantial aggregation in total numbers of parasites in both juveniles and adults ($s^2/\bar{x}$=292.4 and 352.00, respectively). Species numbers, however, were randomly distributed in juveniles ($s^2/\bar{x}$=0.99) and more uniform in adults ($s^2/\bar{x}$=0.65).

Juvenile and adult halibut harbored, on average, 4.0 and 4.0 gastrointestinal (GI) helminth species, 2.1 and 4.1 non-GI species, 0.66 and 2.8 ectoparasite species, and 0.84 and 0.97 myxosporean species, respectively. Juveniles and adults averaged 175 and 149 GI helminths, 10.8 and 135.4 non-GI helminths, 2.1 and 17.3 ectoparasites, respectively.

There was no bimodality in the prevalence category plots (Figure 2.3), but there was a breakpoint at 60% prevalence; therefore, 60% was established as the lower limit for "very common". The lower limit for "common" was set at 40% prevalence because in both juveniles and adults there was an increase in number of

species in this category compared to the 30% category. No parasite species attained 40% prevalence in recruits, but there were 3 common and 2 very common species in juveniles and 6 common and 6 very common species in adults.

The parasite assemblage not only expanded, but also changed as fish grew from the recruit to the juvenile stage. The nematodes *Hysterothylacium aduncum* (prevalence = 25%) and *Ascarophis filiformis* (prevalence about 12%) were the most prevalent parasites in recruits. However, *A. filiformis* declined markedly in the juvenile stage (even in localities contiguous with the sampling localities for recruits). The prevalence of *H. aduncum* increased in the juvenile stage to become one of two very common species. Another recruit species, the acanthocephalan *Corynosoma villosum* (prevalence about 7%) increased in prevalence to become one of three common species in juveniles. The other very common and common species were new to the assemblage (Table 2.2).

Progression to the adult stage was accompanied by more changes in the parasite assemblage. *Corynosoma villosum* and *Anisakis simplex* increased in prevalence to become two of six very common species in adults. The prevalence of *Tubulovesicula lindbergi* declined slightly in adults, but it was still one of the very common species. The other very common species were the monogeneans *Entobdella hippoglossi* and *E. pugetensis* and the copepod *Acanthochondria hippoglossi*. All very common species are present to a much lesser extent in juveniles and absent in recruits. Six more species, all of which are present, but not common, in juveniles, are common in adults (Table 2.2).

In contrast to the general trend of increasing prevalence in larger fish, seven species (the myxosporeans *Ceratomyxa drepanopsettae* and *Kudoa thyrsites*, the digeneans *Hemiurus levinseni*, *Podocotyle gibbonsia*, *Steganoderma formosum*, and *Stenakron vetustum*, and the nematode *H. aduncum*) were at least twice as prevalent in juveniles as compared with adults (Table 2.1). All of the helminths and probably the myxosporeans as well are acquired through consumption of invertebrate intermediate (alternate in the case of myxosporeans) hosts. *Stenakron vetustum* and *S. formosum* also had intensities at least twice as high in juveniles compared to adults. *Hemiurus levinseni* and the nematode *H. aduncum* also had higher intensities in juveniles, but only marginally so.

There were no significant differences in parasite number or species number due to sex in either the whole data set (Mann-Whitney $p = 0.106$, $p = 0.738$), the juvenile size class (Mann-Whitney $p = 0.817$, $p = 0.077$), or the adult size class (Mann-Whitney $p = 0.117$, $p = 0.673$). There was no difference between sexes in species number with either length ($p = 0.379$), age ($p = 0.180$), or weight ($p = 0.379$) as individual covariates. However, females had consistently higher parasite numbers with length ($p = 0.046$), age ($p = 0.023$), or weight ($p = 0.057$) as individual covariates; when age and length were covariates in concert, which essentially controlled for growth rate, there was no difference in parasite number based on sex ($p = 0.389$).

Plots of species richness and abundance versus size for each age class revealed that the number of species generally increased with age and length within age class until age 6, at which point the number of species plateaued (Figure 2.4). The abundance curve (Figure 2.5) showed more variability within and between age classes, no evidence of a plateau, and that larger fish within an age class larger fish generally had more parasites. Also, many of the age-classes (beginning with age 5) exhibited a J-shaped abundance curve. The smallest fish in each of these age classes had more parasites than slightly larger fish. Analysis of the residuals for those fish in the downward part of the J-shaped curves (from a double log regression of mass on length in the total (juveniles and adults) data set) indicated a larger than expected percentage of negative residuals in the 5 and 6 year old fish (Table 2.3). Prediction of a mean weight for the smallest group of fish, from a double log regression of mass on length in the larger fish within an age class, overestimated the actual weight of the 6 and 7 year old fish (Table 2.3).

There were no significant relationships between liver weight and parasite number or species number in either the total (juveniles and adults) data set or the adult fish. In the juveniles there was a significant ($p < 0.1$) negative relationship between parasite number and liver weight , but no relationship with species number (Table 2.4). If the relationships were examined using either internal parasites only or gastrointestinal parasites only, the pattern was the same. Only the negative relationship between worm number and liver weight in the juvenile fish was significant at the $p < 0.1$ level (Table 2.4). However, in all cases the proportion of the variance explained was low.

Cluster analysis revealed that the composition of the parasite community of Pacific halibut is most similar to that of Atlantic and Greenland halibut (Figure 2.6). Pacific flatfishes formed a separate cluster that

was more similar to other Pacific fishes than to the cluster that contained Pacific halibut. With uniquely Atlantic fishes removed from the analysis, Pacific halibut was most similar to Greenland halibut. Arrowtooth flounder and Dover sole joined the cluster containing Pacific halibut. A cluster containing the remaining Pacific flatfishes joined the cluster containing the halibuts (Figure 2.7).

DISCUSSION

My results show that the Pacific halibut is infected by a diverse parasite fauna. Of the 79 parasite taxa now known from Pacific halibut, 32 (indicated by an asterisk in Table 2.1) were first found in this study; 8 of these were rare. *Dissosaccus laevis* is a new Pacific record (but see Love and Moser (1983) cite an unpublished record of *D. laevis* from California). I found 25 of the 47 parasite taxa previously reported from halibut. Of the 22 previously reported taxa I did not find, one was reported only from an aquarium-held host and one was listed as accidental. Seven species (*Progonus muelleri, Lepidapedon gadi, Podocotyle reflexa, Podocotyle atomon, Steringophorus furciger, Corynosoma reductum,* and *Heterobothrium affinis*) I did not find have been reported in halibut only from Kamchatka or the western Bering Sea, though almost all (except *Corynosoma reductum* and *Dinosoma tortum*) have been found in the northeast Pacific in other host species.

In my study there is a group of species that are common or very common in most localities in both juveniles and adults. Three and six species were common in juveniles and adults respectively, and two and six species were very common in juveniles and adults, respectively (Table 2.2). Of the six most common species in halibut in the western Pacific (Mamaev et al. 1963), four (*Corynosoma strumosum, Echinorhynchus gadi, Derogenes varicus*, and *Steganoderma formosum*) are either common or very common in my study. The other two (*Hemiurus levinseni* and *Brachyphallus crenatus*) are present in my study, but common only in a few localities. These patterns suggest that there is a baseline parasite fauna for Pacific halibut. They also suggests that halibut are significant hosts in the life cycles of these parasites.

There are also many parasite species that are either uncommon or rare. Of those parasites from halibut in the western Pacific (Mamaev et al. 1963), four (*Lepidapedon gadi, Podocotyle reflexa, Podocotyle atomon*, and *Steringophorus furciger*) are fairly rare and *Dinosoma tortum* is common in only one locality. This pattern suggests that halibut, wherever they are, sample a wide variety of the parasites available.

Compared with other marine fishes, individual halibut also have a rich and abundant parasite fauna, including more species and individuals than found in almost all other marine fishes from temperate North America (Table 2.5). Halibut are also at or near the top of the measures for each category of parasite (non-GI helminths, ectoparasites, and myxosporeans/protozoans) (Table 2.5). Patterns in gastrointestinal parasites of

marine fishes have been more extensively studied. Halibut again fall at the upper end of the spectrum for both numbers of species and numbers of individuals (Figure 2.8).

Why do halibut have rich, abundant parasite communities? Polyanski (1961) suggested that larger, more mobile and gregarious fishes, and those that eat a variety of foods have more parasites. Therefore, in the following paragraphs I examine the roles of these potential determinants of parasite community composition and abundance. Two kinds of data are used to support my conclusions. Data on gastrointestinal (GI) parasites are shown in Figure 2.8 (letters designate the hosts referred to in the following discussion). Other information is provided in Table 2.5. Common names for those species not listed in Materials and Methods are provided.

The most obvious feature that may influence the parasite community is host size. Indeed, Poulin (1995), among others, has shown size to be an important determinant of parasite communities in fishes. Larger hosts generally consume more food, and thus may be exposed to more parasites, both species and individuals. Large hosts also have more space available for exploitation by parasites. Pacific halibut (Table 2.5, Pac. hal.) and *Reinhartdius hippoglossoides* (A) are among the largest hosts in the comparisons. They also have the most parasites (in virtually every category). However, size by itself is only a partial determinant. Other large hosts such as *Hippoglossus hippoglossus* (B) and *Atherestes stomias* (Table 2.5, C) appear to have much simpler communities while smaller hosts like *Sebastes nebulosus* (china rockfish) (D) have rich and abundant parasite communities.

Large hosts are usually long-lived ones, but some smaller species are also long-lived. Age by itself would likely be an important factor for those parasites that accumulate with time (primarily the non-GI helminths). Pacific halibut, *R. hippoglossoides* (A), *Anoplopoma fimbria*, and some of the rockfishes (*Sebastes paucispinis* (bocaccio) and *Sebastes ruberrimus* (yelloweye rockfish)), all long lived species, have rich non-GI communities (Table 2.5). Age by itself is not likely to have an effect on most GI parasites or ectoparasites because their generation time is short relative to the generation time of the fish, so that they would not accumulate.

My data on Pacific halibut suggest that growth rate, rather than size or age, is the most important determinant of the parasite fauna. Fish that are growing faster consume more food and thus are probably

exposed to more parasites. High growth rate, however, does not guarantee a rich fauna. *Oncorhynchus tshawytscha* (H) grows very rapidly, but has a relatively poor parasite fauna.

More mobile fish would be likely to traverse more habitats and encounter a larger variety of parasites, but fewer individuals of each. In addition, by the time those parasites produce eggs a mobile host may have left suitable habitat, thus reducing the efficiency of transmission. Data from halibut support this idea. Halibut are extremely mobile (NOAA 1990) and have an extensive list of parasites. However, most of the parasites in halibut are relatively rare, and those that are common are those that are transmitted broadly to a wide range of hosts. Similarly, salmon (H, I) which are extremely mobile, have relatively simple parasite communities. On the other hand, resident fish with low mobility may facilitate efficient cycling of parasites. *Sebastes nebulosus* (D) is not very mobile and has rich communities dominated by locally transmitted parasites.

Gregariousness would likely facilitate those parasites transmitted directly between fish, particularly ectoparasites. The data for ectoparasites are limited; *Sebastes alutus* (Table 2.5) is a schooler and has a rich ectoparasite community whereas *Clupea pallasi*, another schooler, (Table 2.5) does not appear to have many ectoparasites. In contrast, halibut do. This may be because my samples were taken in the summer when halibut congregate on feeding grounds. With respect to GI parasites, the effect of gregariousness is unclear. If fish are congregated on feeding grounds, then many fish in a sample may contain large numbers of the same types of locally transmitted parasites. This would appear to be the case in halibut and perhaps for *Gadus morhua* (K). Territoriality, surprisingly, may create a similar pattern. Territoriality would facilitate those parasites that can cycle locally, which would include not only ectoparasites, but others as well. Some rockfishes (*Sebastes elongatus* [greenstriped rockfish] (L), *S. paucispinis* (F), and *S. ruberrimus* (G)) (Table 2.5), which are territorial, have rich and abundant ectoparasite infestations. The last two, and *S. nebulosus*, have a rich GI fauna, probably for the same reasons. However, depending on how localized transmission is, one might expect great variability among individual fish from a locality. This appears to be the case for *S. nebulosus* (Holmes 1990).

Holmes (1990) showed that diet type was not important in determining the complexity of the GI parasite community in marine fishes. However, diet will certainly influence the types of parasites present.

Fishes with opportunistic diets would be likely to acquire a variety of parasites. Pacific halibut, *R. hippoglossoides* (Table 2.5, A), *G. morhua* (K), and *Theragra chalcogramma* (Table 2.5, M) are all opportunistic feeders and also have reasonably rich parasite communities, but *A. stomias* (Table 2.5, C), which is also an opportunistic feeder, does not. Pacific halibut and *S. nebulosus* have different diets and different types of parasites (see Holmes 1990 for helminth fauna of *S. nebulosus*). The parasites dominant in *S. nebulosus* are rarely, if at all, found in halibut. The most common parasites in *S. nebulosus* are relatively specific and are those that are acquired from invertebrates. Halibut parasites are some of the most common marine parasites and are largely acquired from fish, since halibut are high in the food web. The two fish, however, both have rich GI communities.

Overall, this analysis suggests that no one factor is predominant in determining the parasite community composition and abundance in marine fishes. In fact, composition and abundance may be created by different sets of interacting factors. The halibut's rich community is created due to the fact that the animals are large, live long lives, have a diverse opportunistic diet, and are not territorial, but do congregate on feeding grounds. Age and size would be influential in determining abundance, particularly for the non-GI parasites. There may also be more ectoparasites on larger hosts. Mobility and diet would influence the kinds of parasites. Indeed, I have shown that halibut harbor a large variety of parasites that come from a variety of sources. *Sebastes nebulosus*, on the other hand, has a rich community for different reasons. Diet determines the types of parasites present. Territoriality produces high, but variable, populations of specific GI helminths that cycle more locally. Other rockfishes have rich ectoparasite communities because those parasites don't require intermediate hosts and can recycle in the territory. Other rockfishes also have reasonably abundant non-GI parasites, though not as abundant as in larger fishes. Long lives and a moderate size may produce this pattern.

Other factors not covered by Polyanski may also be very important. Holmes (1990) (using freshwater fish data from Kennedy et al. 1986) showed that marine fishes have parasite communities with more species, but similar numbers of individuals as freshwater fishes (Figure 8). I found that halibut had about the same number of individuals, but more species, as in heavily infected freshwater fishes. Holmes (1990) believed that the greater vagility of marine hosts and their prey compared to freshwater fishes was important in

explaining the differences between marine and freshwater fishes. Probably more important is that patterns of transmission differ markedly between freshwater and marine systems (Marcogliese 1995). He attributed many of these differences to the increased complexity of the marine food web compared to that in the freshwater environment. Ewald (1995) noted that some hosts are used as resources and others simply as agents of transmission. In an open, complex marine food web, parasites may be able to use a much wider variety of hosts as both. The parasites may be able to use several alternative pathways to the definitive host, and hosts may be expected to have more species of parasites, many of which may be juvenile stages.

Pacific halibut harbor 16 species of juvenile, non-GI helminths including 5 nematodes, 5 cestodes, 2 digeneans, and 4 acanthocephalans. Many of these species are among the most common and abundant parasites found in marine fishes. Thoney (1991) found that non-GI parasites were not a significant part of the parasite communities in spot (*Leiostomus xanthurus*) and croaker (*Micropogonias undulatus*). However, he examined only juveniles. Most of the non-GI parasites in my study are, indeed, less common in juveniles and recruits, but they are always present and form a significant portion of the community. Thoney (1991) hypothesized that he saw few parasites (GI and non-GI) because he was working in estuaries, which have less diverse faunas than open marine systems. Further, because spot and croaker feed primarily on invertebrates, acquisition of juvenile stages from fishes would be less common than in a piscivore like halibut. These patterns suggest that, in addition to the factors discussed by Polyanski (1961), the richness of parasites in halibut reflects the increased importance, as intermediate hosts, of marine fishes compared to freshwater fishes and the increased ability of marine parasites to be transferred trophically from prey fishes to predator fishes.

Interestingly, most of the juvenile stages of parasites in halibut are probably dead ends. Unlike many other marine fishes, halibut are not likely to serve as significant intermediate or transport hosts for many parasites because halibut (adults and probably a significant portion of larger juveniles) are not known to be significant natural food items for any predators (Best and St-Pierre 1986). Halibut are large, powerful, non-schooling, and demersal animals that are less accessible to predators than smaller schooling, pelagic species (Best and St-Pierre 1986). Killer whales and narwhals are predators of halibut, but stomach analyses suggest that halibut are a minor prey (Best and St-Pierre 1986). Seals, sea lions, and sharks are known to take halibut from fishing gear and thus may provide some opportunity for parasite transfer. Eight of the species of juveniles

(*Anisakis simplex*, *Contracaecum* sp., *Pseudoterranova decipiens*, Spirurid gen. sp., *Bolbosoma* sp., *Corynosoma enhydri*, *C. strumosum*, and *C. villosum*) mature in birds or mammals and eight (*Otodistomum* sp., *N. surmenicola*, *Scolex pleuronectis* (both forms), Tetraphyllidea sp., Trypanorhyncha sp., *Hysterothylacium aduncum*, and bucephalid metacercariae) mature in fish. Of the parasites that mature in birds and mammals, 2 are certain dead ends (*Corynosoma enhydri* matures in sea otters and Spirurid gen. sp. probably matures in birds). The others mature in whales or seals. Of those that mature in fishes, *H. aduncum* is the least likely to be a dead end, primarily due to its abundance in small halibut and its use of halibut as a definitive host as well. The six species (*Otodistomum* sp., *N. surmenicola*, *S. pleuronectis* (gall bladder form), *S. pleuronectis* (intestinal form), Tetraphyllidea sp., and Trypanorhyncha sp.) that mature in elasmobranchs are not certain dead ends.

Another factor in the richness and abundance of halibut parasite communities may be the overall lack of specificity in the marine system. Nine of the 14 very common and common parasites in juveniles and adults (*T. lindbergi*, *H. aduncum*, *A. simplex*, *C. villosum*, *C. strumosum*, *N. surmenicola*, *D. varicus*, *E. gadi*, and *S. pleuronectis* (intestinal form)) are generalist species found in a wide variety of marine fishes. Less abundant parasites (prevalence ≤ 30%) are mostly generalists. Holmes (1990) and Arthur and Albert (1994) considered specificity to be a minor contributor to the parasite communities they examined. I also find few strictly host-specific parasites in Pacific halibut. The myxosporeans and copepods appear to be more host-specific than other parasites. *Leptotheca* sp., which may be a new species, may be specific. *Acanthochondria hippoglossi*, *Ceratomyxa drepanopsettae*, *C. platichthys*, *Entobdella hippoglossi*, *Aporocotyle simplex*, and *Paracapillaria parophrysi* appear to be specific to pleuronectids. *Steganoderma formosum*, *Stenakron vetustum*, *P. gibbonsia*, *Cucullanus heterochrous*, *Myxidium incurvatum*, and *Unicapsula muscularis* appear to have some predilection for pleuronectids (information based on checklists such as Margolis and Arthur (1979) and McDonald and Margolis (1995)). Only 5 of the very common or common parasites and less than 25% of the less abundant species are broadly specific to pleuronectids. Bush (1990) hypothesized that this lack of specificity was an adaptation to increase the probability of completing the life cycle in an open marine habitat.

There is, however, as Holmes (1990) suggested, evidence of specificity at larger taxonomic scales. The closest relatives of Pacific halibut are the Atlantic halibut (*H. hippoglossus*), Arrowtooth flounder (*A. stomias*) and Greenland halibut (*R. hippoglossoides*). Pacific halibut is less closely related to other flatfishes. In the cluster analysis that includes Atlantic species, the parasite faunas of the three species of halibuts form a cluster. The other flatfishes form their own cluster. This may indicate some phylogenetic specificity. The halibuts are also similar ecologically suggesting that both ecology and phylogenetics play a role in producing this pattern. The halibut cluster joins a cluster of two Atlantic gadids (haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*G. morhua*)). Both are large, mostly piscivorous, and well-studied, with long lists of parasites. In the analysis limited to Pacific fishes, the clustering of flatfishes strongly suggests an important role of phylogeny. Greenland halibut and, particularly, Arrowtooth flounder are the most similar to Pacific halibut in both phylogeny and ecology, and cluster with it. Many of the other Pacific flatfishes, which join the halibut cluster, are ecologically different; therefore, their inclusion in the cluster is strongly indicative of phylogenetic affinities. Further, species such as sablefish (*A. fimbria*) and chinook salmon (*O. tshawytscha*), which have similar food habits to Pacific halibut, are not included in the halibut cluster. Dover sole (*Microstomus pacificus*) is more ecologically and phylogenetically related to the other Pacific flatfishes, but joins the halibut cluster. Dover sole are large and well-studied, like cod and haddock in the analysis containing Atlantic species, and their inclusion in the halibut cluster may be explained by these factors.

A closer look at Pacific halibut

The species richness of the community in individual halibut develops over a 6-7 year period then remains relatively stable thereafter. Abundance is more variable and shows no evidence of an asymptote. However, halibut attain a much greater size and age than represented in my sample, therefore, abundance may stabilize in the largest fish. Changes in the parasite fauna over the life history of halibut are related to changes in diet and habitat. Recruits live in shallow inshore areas and eat primarily small crustaceans. They are, in turn, infected with parasites that use crustaceans as intermediate hosts. The primary parasites of this size group

(*H. aduncum*, *A. filiformis*, and *C. villosum*) cycle through crustaceans. As fish age they move to deeper water and their diet broadens to include a wider variety of invertebrates and fishes. *Ascarophis filiformis* disappears due to a decrease in the importance of euphausiids in the diet. The prevalence of *H. aduncum*, which cycles through a variety of zooplankters and may be acquired from fishes via trophic transfer, increases due to this diet shift. Subadults/adults have similar kinds of parasites as juveniles. However, adults generally have additional species and infections of higher prevalence and intensity. This is particularly true for non-GI and ectoparasitic species but, interestingly, not true for GI species. Several species, including a number of the Hemiuroids, the trematodes *Podocotyle gibbonsia* and *S. formosum*, the nematode *H. aduncum*, and the myxosporeans *Leptotheca* sp., *C. drepanopsettae*, and *Kudoa thrysites*, have noticeably higher prevalences and intensities (non-myxosporeans) in juveniles. These patterns in endoparasites are reflective of the decreasing importance of crustaceans and the increasing importance of fish in the diet. As fish grow they eat fewer crustaceans and, as a result, have fewer of the parasites that cycle through crustaceans. The relatively constant number of GI species, but their decreasing intensities in adults is indicative of trophic transfer. The acquisition of individuals is slowed by the decreasing importance of crustaceans in the diet, but trophic transfer maintains the species in the community. With respect to the myxosporeans, the relatively constant number of species in adults and juveniles suggests that the myxosporeans are acquired largely from invertebrates and that infections are of long duration. Similar patterns of changes in parasite faunas associated with changes in diet and habitat have been demonstrated in a number of fishes (Polyanski 1961; Thoney 1991; Belghyti et al. 1994).

Correlations in my data indicate that host size and age are significant determinants of numbers of parasite individuals and species in halibut. Given that a large portion of the parasite fauna in halibut is trophically transferred and long-lived, it is not surprising that halibut accumulate more species and, particularly, individuals as they grow and age. Moreover, it is apparent from my data that growth rate is a primary determinant of the parasite community (particularly for abundance). Larger fish within an age-class have more parasites. It is likely that larger fish have grown faster, eaten more and therefore been exposed to more parasites. In addition, age and size of halibut are intercorrelated with sex. Female halibut grow more quickly than males, are larger than males for a given age, and live longer than males. Females, indeed, have

more parasites until both size and age are controlled. Des Clers (1991) attributed the size-related increase of *Pseudoterranova decipiens* in Atlantic cod to the increased trophic needs of larger fish. Larger fish also may have more space available in which parasites can accumulate. Space availability may be particularly important for those parasites that accumulate in the body cavity. Polyanski (1961), George-Nascimento (1987), Belghyti et al. (1994) (and references therein) cite several other examples of the relationship between diet, host size, and parasitism.

According to Rohde (1993), effects of parasites on hosts range from virtually nothing to death. May (1983) discussed the ability of parasites to regulate host populations and concluded that although parasites may play a role in population regulation, they are simply one of many factors. The majority of reported severe pathologies and deaths are often associated with stress and poor environmental conditions under culture conditions (Rohde 1993, Kent et al. 1994). Indirect effects, which are more likely to be operating in my system, are harder to evaluate. The apparent J-shape of the abundance curve within age-classes may be indicative of decreased condition due to parasites. The smallest fish within each age-class often have more parasites than slightly larger fish within the same age-class. Large fish in the same age class have grown faster (i.e., eaten more) and, as a result, have been exposed to more parasites. However, that argument cannot explain more parasites in the smallest fish. My interpretation is that these smallest fish are debilitated (possibly by parasites) and are likely to be in poor condition. The fact that the smallest fish in the 5 and 6 year old classes have negative bias in their regression residuals and that the 6 and 7 year old classes weigh less than predicted for their size supports this interpretation. The marginally significant negative correlation between the number of intestinal worms and liver weight in the juveniles (Table 2.4) also is consistent with this interpretation of the J-shape of the abundance curve. Marine fishes often use the liver as a fat storage organ; therefore, liver weight may be used as an index of condition. The absence of this pattern in the older age classes suggests that these heavily parasitized fish are lost from the population.

Alternatively, the significance of the J-shape in the 5, 6, and 7 year olds may be related to the transition to the adult lifestyle. At these ages fish may be maturing, and diet and habitat are changing. As a result, the dip in the curve may be the lag between the loss of the juvenile fauna and the acquisition of the adult fauna. The lack of a significant J-shape in the 8-11 year old categories (all with sample sizes at least as large

as the 5, 6, and 7 year old categories) may support this interpretation because many of these fish would have already made the transition. If this is the case, I might expect a similar, or at least consistent, pattern in the accumulation of species. However, as indicated, the accumulation of species shows no such pattern. The plateau is already taking shape in the 5-7 year old categories. Further, I have shown that a significant portion of the transition to the adult fauna is the increase in the abundance of species that are already present. In addition, the lack of the J-shape in the 8-11 year old categories may not be entirely inconsistent with the interpretation of parasite-induced mortality. It may be reasonable to expect that if parasites are associated with condition, mortality may occur early and that once fish survive past a certain point the probability of parasite induced mortality decreases. Therefore, I interpret the J-shape as evidence of decreased condition.

Three (27%) of the species that are more prevalent in juvenile halibut than adult halibut are myxosporeans. Twenty-one of 25 documented diseases of marine fishes listed by Rohde (1993) are caused by protozoans or myxosporeans. Some species of *Ceratomyxa*, such as *C. shasta* in salmonids, are known pathogens (Bartholomew et al. 1989). *Kudoa* has been linked to extensive muscle tissue damage in Atlantic salmon and a significant host response in Pacific hake (Kent et al. 1994). The effects of *Unicapsula* are undocumented, but the presence of pseudocysts in muscle tissue provides a potential for detrimental effects. Pathogenic effects of macroparasites (helminths) are often related to intensities. *Anisakis* spp. and *H. aduncum* have been linked (albeit questionably) to host liver problems and weight loss (Petrushevski and Shulman 1961). Their migration through the viscera is potentially damaging. The commonness of *H. aduncum* in the juveniles provides increased opportunity for damage. These are the species most likely to be responsible for the debilitation of the smallest fish.

It is possible that debilitation is a major factor determining the number of parasites, equivalent to size, mobility, gregariousness, and diet. Presumably, this would operate through increased susceptibility to those parasites to which a fish is exposed. Indeed, fish debilitated by poor environmental conditions have been shown to be immunosuppressed and more susceptible to a variety of parasites (reviewed in Pickering 1987). In turn, heavy parasitic infections would further decrease condition and increase susceptibility to other diseases, environmental conditions, and parasites (Boyce and Behrens-Yamada 1977; Boyce 1979). Therefore,

parasites may be very important in increasing the variability in a population, the net result of which is that those hosts at the lower end of the scale are less competitive and lost from the population (Steinwascher 1979a, b).

Table 2.1. Parasites of three size classes of Pacific halibut, *Hippoglossus stenolepis*, from the North American Pacific coast.

Parasite	Recruits (5-10 cm) n=104		Juveniles (10-55 cm) n=104		Subadults/adults (>55 cm) n=328	
	Prev. (%)	Intensity±SD	Prev. (%)	Intensity±SD	Prev. (%)	Intensity±SD
MYXOSPOREA						
*Ceratomyxa drepanopsettae**			12.5		3.05	
*Ceratomyxa platichthys**			12.5		42.59	
Kudoa thyrsites			22.1		3.35	
Leptotheca sp. (urin)*			29.8		22.26	
Leptotheca sp. (gb)					2.43	
*Myxidium incurvatum**			5.8		10.37	
Unicapsula muscularis			1.0		7.0	
*Zschokella sp.**					0.3	
MONOGENEA						
Entobdella hippoglossi			25.0	2.1±1.2	85.9	7.5±8.2
*Entobdella pugetensis**			28.9	5.0±5.2	87.8	8.7±12.6
DIGENEA						
Aporocotyle simplex			7.7	1.8±0.9	19.8	1.5±1.0
Brachyphallus crenatus			22.1	9.1±18.3	16.8	8.5±14.6
Bucephalid metacercariae*†					5.2	2.5±2.8
Derogenes varicus	1.0	1.0±0.0	16.4	1.8±1.1	46.3	9.6±21.8
*Dissosaccus laevis**			1.0	1.0	3.7	5.3±7.3
*Genolinea laticauda**					1.2	1.5±0.6
*Gonocerca phycidis**					4.3	1.4±1.16
Hemiurus levinseni			14.4	2.7±2.8	7.6	1.7±1.6
*Lampritrema sp.**					0.3	1.0
Lecithaster gibbosus			5.8	3.0±4.0	13.4	9.5±20.1
*Lecithophyllum botryophorum**					0.3	1.0±0.0
*Lepocreadium sp.**					0.9	1.0±0.0
Otodistomum sp.*†			1.9	1.5±0.7	15.9	11.9±21.1
Parahemiurus merus			4.8	1.0±0.0	0.9	1.3±0.6
*Podocotyle gibbonsia**	1.9	1.0±0.0	19.2	29.2±33.3	8.2	28.6±45.9

Table 2.1 (continued)

Parasite	Recruits (5-10 cm) n=104		Juveniles (10-55 cm) n=104		Subadults/adults (>55 cm) n=328	
	Prev. (%)	Intensity±SD	Prev. (%)	Intensity±SD	Prev. (%)	Intensity±SD
*Podocotyle sinusacca**					2.1	2.1±1.9
*Prosorhynchoides basargini**			20.2	6.7±8.2	24.4	8.8±24.8
Prosorhynchus sp					2.7	2.8±3.9
Pseudopecoelus nossamani			1.0	1.0	0.3	2.0
Steganoderma formosum			46.2	11.3±18.3	25.0	3.5±12.2
Stenakron vetustum			8.7	3.2±4.2	0.3	1.0
Tubulovesicula lindbergi			88.5	160.0±241.4	79.9	134.7±249.5
*Zoogonus dextrocirrus**					0.3	1.0
unidentifiable Digenea					0.6	1.0±0.0
CESTOIDEA						
*Bothriocephalus scorpii**			2.9	2.0±1.0	0.6	1.5±0.7
Nybelinia surmenicola†			11.5	6.1±14.6	39.0	15.8±54.3
Scolex pleuronectis (int)†			37.5	31.5±49.6	48.5	22.6±175.8
Scolex pleuronectis (gb)†			12.5	2.4±1.8	26.2	6.7±8.0
unidentified Trypanorhych†			1.0	1.0	0.3	282
unidentified Tetraphyllidean†			1.9	1.0±0.0	1.2	14.0±21.7
NEMATODA						
Anisakis simplex†			43.3	7.1±28.6	99.4	106.7±215.7
*Ascarophis filiformis**	11.5	1.1±0.3	4.8	9.8±18.1		
*Capillaria margolisi**					7.0	22.9±40.7
Contracaecum sp.†			7.7	2.1±2.8	23.2	2.9±2.9
Cucullanus heterochrous			1.0	2.0	4.3	4.9±11.2
*Hysterothylacium aduncum**‡	25.0	1.5±0.8	68.3	5.2±7.4	31.7	4.0±4.5
*Paracapillaria parophrysi**			4.8	1.6±1.3	19.2	56.5±121.1
Pseudoterranova decipiens†			10.6	2.0±1.8	35.4	2.3±2.0
Spirurida gen. sp. larvae*†			1.0	2.0	7.3	4.3±13.4
unidentifiable nematode†	4.8	1.0±0.0				
ACANTHOCEPHALA						
Bolbosoma sp.*†			1.0	1.0	2.1	1.4±0.5
*Corynosoma enhydri**†			1.9	1.0±0.0	0.6	1.0±0.0

Table 2.1 (continued)

Parasite	Recruits (5-10 cm) n=104		Juveniles (10-55 cm) n=104		Subadults/adults (>55 cm) n=328	
	Prev. (%)	Intensity±SD	Prev. (%)	Intensity±SD	Prev. (%)	Intensity±SD
Corynosoma strumosum†			16.4	1.4±0.9	41.8	7.4±14.6
*Corynosoma villosum**†	6.7	1.3	43.3	6.1±15.9	91.5	16.2±29.4
Echinorhynchus gadi			26.9	4.6±6.4	42.7	6.3±9.6
CRUSTACEA						
Acanthochondria hippoglossi			7.7	1.3±0.5	60.1	3.2±2.8
Gnathiid larvae*†			1.0	1.0	5.8	2.5±2.7
*Lepeophtheirus bifidus**					0.3	1.0
*Lepeophtheirus hospitalis**					0.3	1.0
Lepeophtheirus parviventris			1.0	1.0±0.0	14.9	1.3±0.8
Lepeophtheirus pravipes			1.9	1.0±0.0		
*Opisa tridentata**					17.7	5.1±10.5
HIRUDINOIDEA						
unidentified leeches			1.0	1.0	2.1	1.3±0.8

* - New record for Pacific halibut

† - Juvenile stage

‡ - Juveniles in recruits, juveniles and adults in juvenile and adult fish

Table 2.2. Most common parasite species in three size classes of Pacific halibut.

Recruits	Juveniles	Adults
	Very Common (>60%)	
	Hysterothylacium aduncum †	*Tubulovesicula lindbergi* §
	Tubulovesicula lindbergi §	*Anisakis simplex* ‡
		Corynosoma villosum ‡
		Entobdella hippoglossi ‡
		Entobdella pugetensis ‡
		Acanthochondria hippoglossi ‡
	Common (40-50%)	
	Steganoderma formosum †	*Corynosoma strumosum* ‡
	Corynosoma villosum ‡	*Echinorhynchus gadi* ‡
	Anisakis simplex ‡	*Nybelinia surmenicola* ‡
		Scolex pleuronectis (intestine) ‡
		Derogenes varicus ‡
		Ceratomyxa platichthys ‡
Important species		
Hysterothylacium aduncum (25%) †		
Ascarophis filiformis (12%) *		
Corynosoma villosum (7%) ‡		

* - parasites most common in recruits

† - parasites most common in juveniles

‡ - parasites most common in adults

§ - parasites roughly equivalent in juveniles and adults

Table 2.3. Regression residual analysis of smallest fish within each age class of Pacific halibut, *Hippoglossus stenolepis*, with a sample size greater than 20 and predicted mean weight ± 95% confidence interval for smallest fish based on a regression of mass on length for the largest fish in the age class.

Age class	n (large fish)	n (small fish)	No. negative residuals (small fish)	Predicted log mean wt. ± 95% C.I. for n small fish	Actual log mean wt. of n small fish
5	10	11	10*	0.17±0.10	0.09
6	21	8	8*	0.19±0.04	0.11†
7	33	5	3	0.29±0.03	0.19†
8	52	10	5	0.5±0.024	0.58
9	36	25	12	0.64±0.026	0.70
10	33	16	7	0.74±0.03	0.73
11	42	5	2	0.75±0.05	0.74

* - significantly greater than expected number of negative residuals (sign test)

† - significantly lower than predicted (outside lower confidence interval)

Table 2.4. Partial correlations for the relationship between liver weight and number of parasite species or number of parasite individuals, given fish length and fish age. Significance assumed at p = 0.1

			$r_{partial}$		p	
Parasite dataset†	Fish sample	n	species	individuals	species	individuals
All species	Juveniles and Adults	407	0.009	-0.024	>0.5	>0.5
	Juveniles	88	0.084	-0.183	>0.2	~0.07*
	Adults	319	0.02	0.047	>0.5	>0.2
GI, body cavity species	Juveniles and Adults	407	0.001	-0.084	>0.5	~0.09*
	Juveniles	88	-0.067	-0.187	>0.5	~0.07*
	Adults	319	0.029	-0.009	>0.5	>0.5
GI species	Juveniles and Adults	407	0.002	-0.057	>0.5	>0.2
	Juveniles	88	-0.137	-0.182	~0.2	~0.07*
	Adults	319	0.054	-0.006	>0.2	>0.5

* = significant result

† = Myxosporeans not included in analyses of relationships with number of parasite individuals

Table 2.5. Comparisons of mean numbers of species and individuals of non-GI helminths, ectoparasites, and myxosporeans/protozoans among various fish species. See text for sources of data and method of calculation.

Fish species	$\bar{x}$ non-GI species	$\bar{x}$ non-GI parasites	$\bar{x}$ species ectos	$\bar{x}$ no. ectos	$\bar{x}$ species Myxos/Protos	Total species*	Total individuals*
Hippoglossus stenolepis	4.9	398	2.3	13.7	1.5	14.1	792.7
Reinhardtius hippoglossoides	3.1	58.1	0.5	0.8	2.7	10.5	1076.9
Theragra chalcogramma	4.0	110.2	0.2	0.8	0.8	9.8	224
Sebastes fasciatus	1.5	33.8	0.1	1		3.5	38.3
Sebastes marinus	1.4	30.7	0.5	1.2		3.5	46.7
Sebastes mentella	1.0	33.8	0.1	0.2		2.3	38.6
Anoplopoma fimbria	1.3	106.2	0.5	2.5		2.83	117.8
Pleuronectes vetulus	0.3	0.5	0.3	0.5	0.7	2.1	19
Microstomus pacificus	1.7	11.2	0.2	0.5	1.1	5.5	36.2
Atherestes stomias	3.6	2.1	0.4	0.8	3.3	4.8	8.3
Pleuronectes bilineatus			0.5	2.3	1.4		

Table 2.5 (continued)

Fish species	$\bar{x}$ non-GI species	$\bar{x}$ non-GI parasites	$\bar{x}$ species ectos	$\bar{x}$ no. ectos	$\bar{x}$ species Myxos/Protos	Total species*	Total individuals*
Clupea pallasi	2.3		0.5		0.8		
Sebastes alutus	2.6	7.9	4.4	60.7		10.3	80.7
Sebastes elongatus	1.7	9.6	1.9	3.3		6.1	20.1
Sebastes paucispinis	1.3	94.2	1.0	18.3		7.3	256.3
Sebastes ruberrimus	2.3	68.8	3.6	13.7		10.8	107.8

* - includes gastrointestinal helminths.

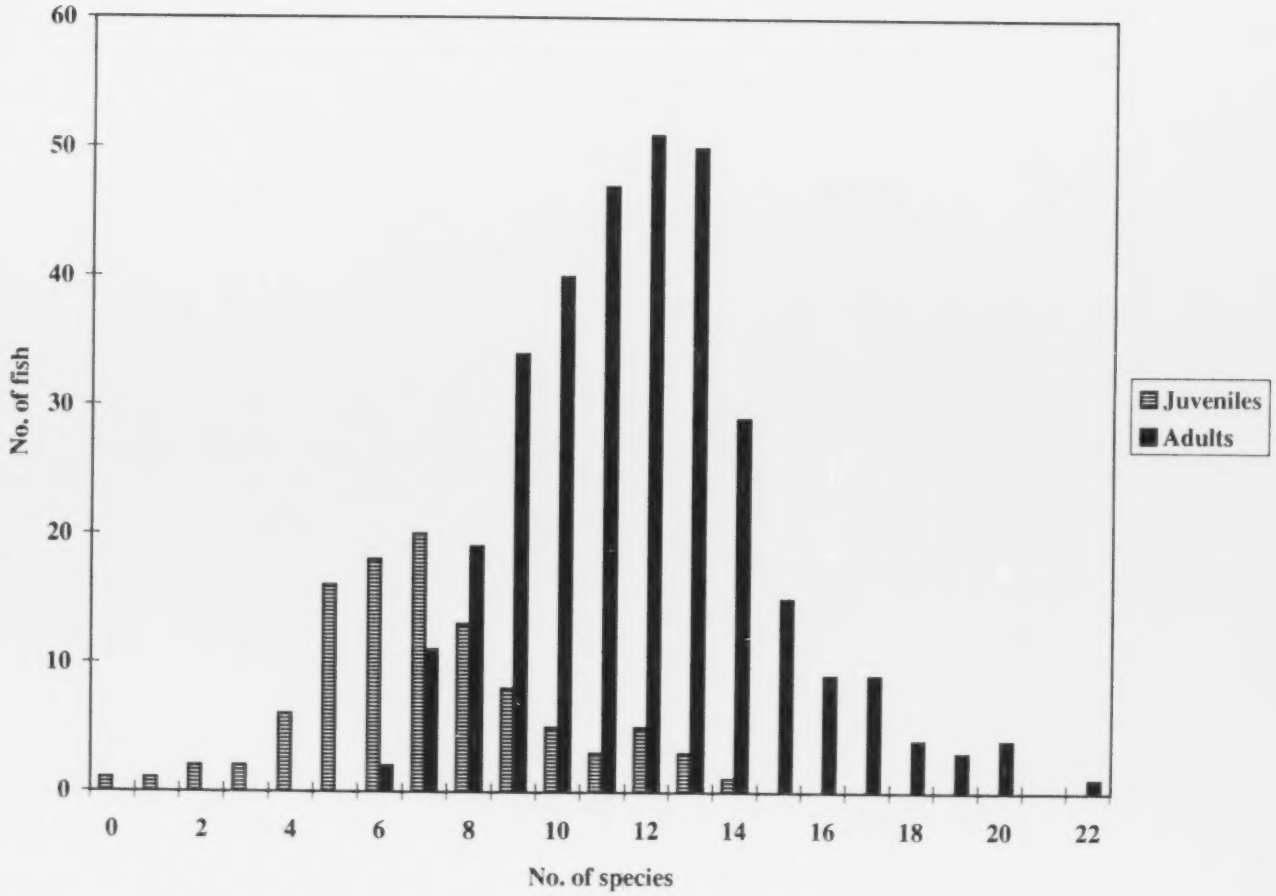

Figure 2.1. Frequency distribution of parasite species in juvenile and adult Pacific halibut, *Hippoglossus stenolepis*.

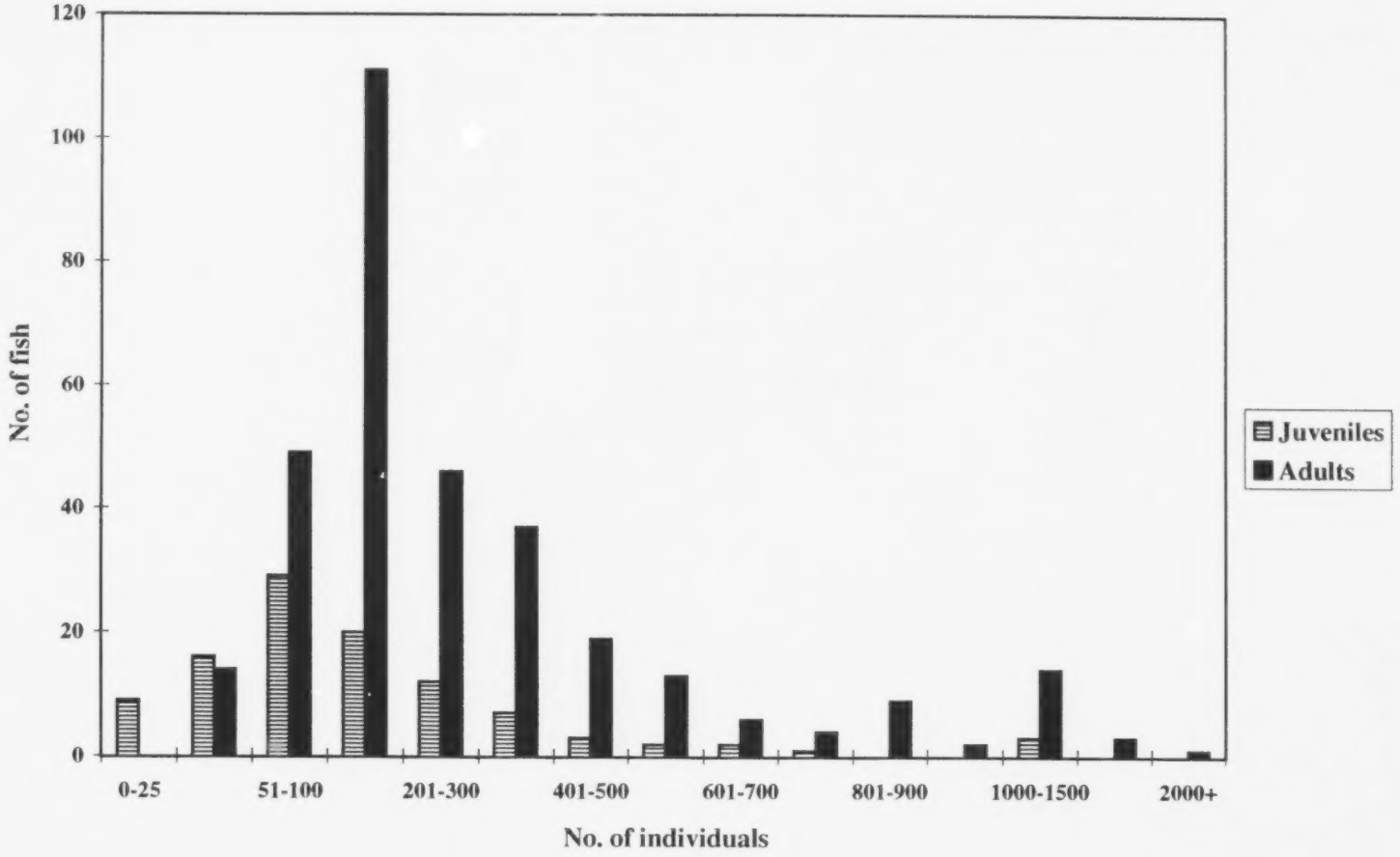

Figure 2.2. Frequency distribution of parasite individuals in juvenile and adult Pacific halibut, *Hippoglossus stenolepis* .

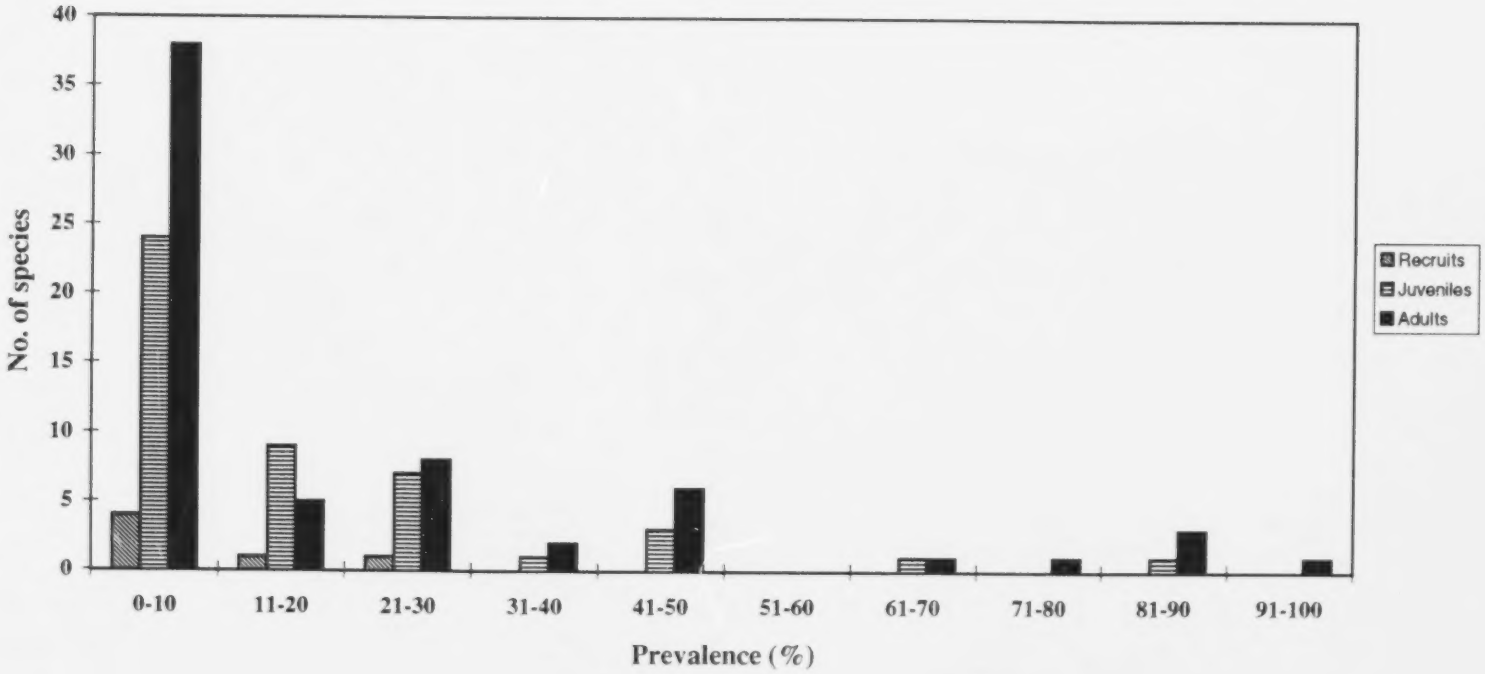

Figure 2.3. Number of species per prevalence category for recruits (<10 cm), juveniles (10-55 cm), and adults (>55 cm) of Pacific halibut, *Hippoglossus stenolepis*.

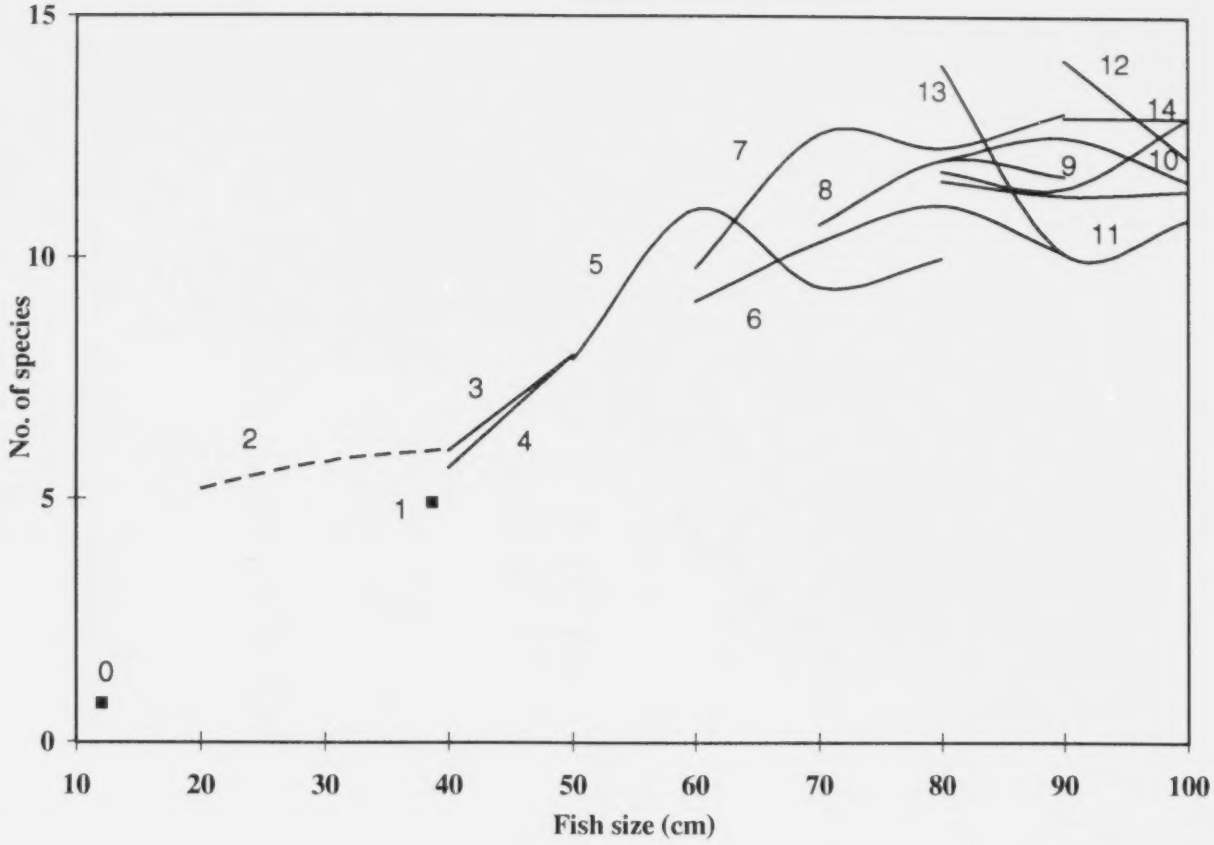

Figure 2.4. Mean numbers of species by length per age class of Pacific halibut, *Hippoglossus stenolepis*. Dotted line is extrapolation between known points.

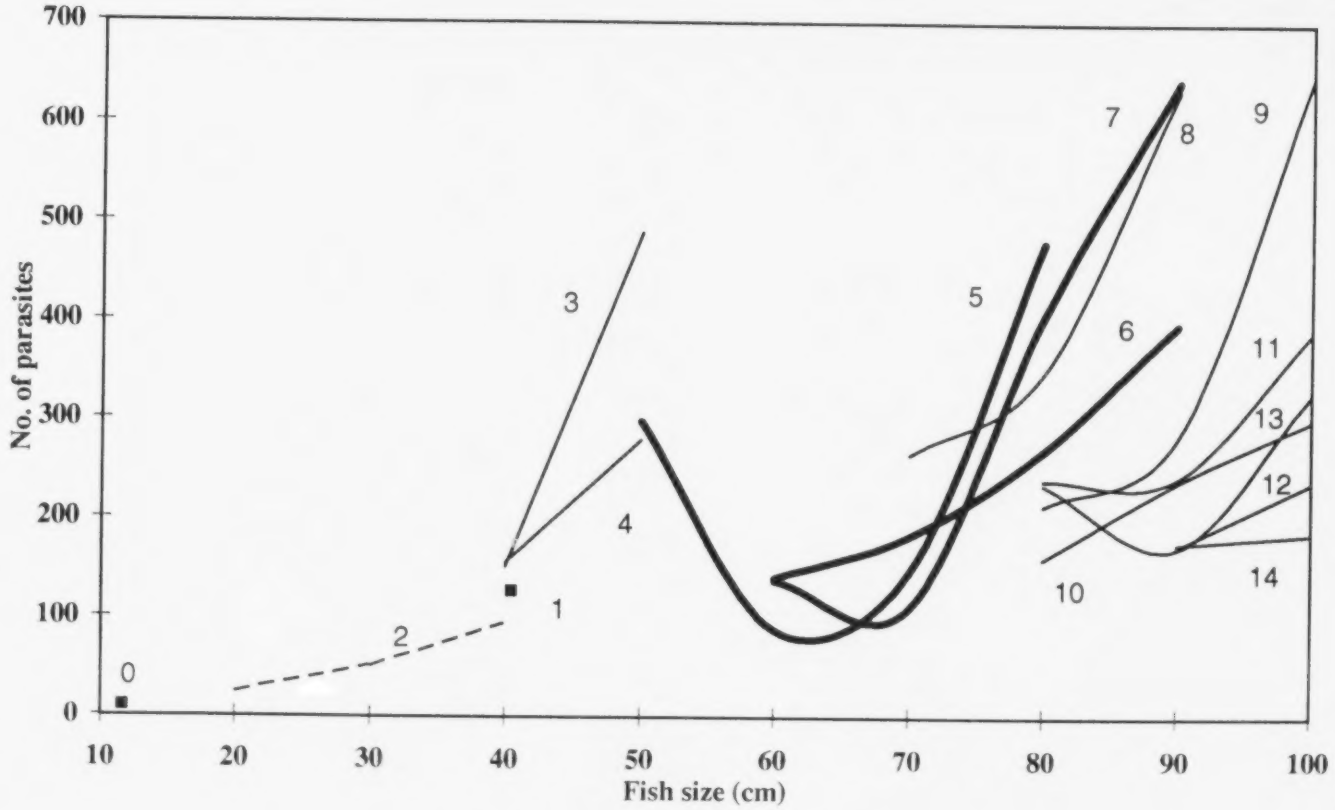

Figure 2.5. Mean numbers of parasite individuals by length per age class of Pacific halibut, *Hippoglossus stenolepis*. Age classes in which small fish show negative bias in the regression residuals and/or lower than expected weight for their size are shown in bold. Dotted line is extrapolation between known points.

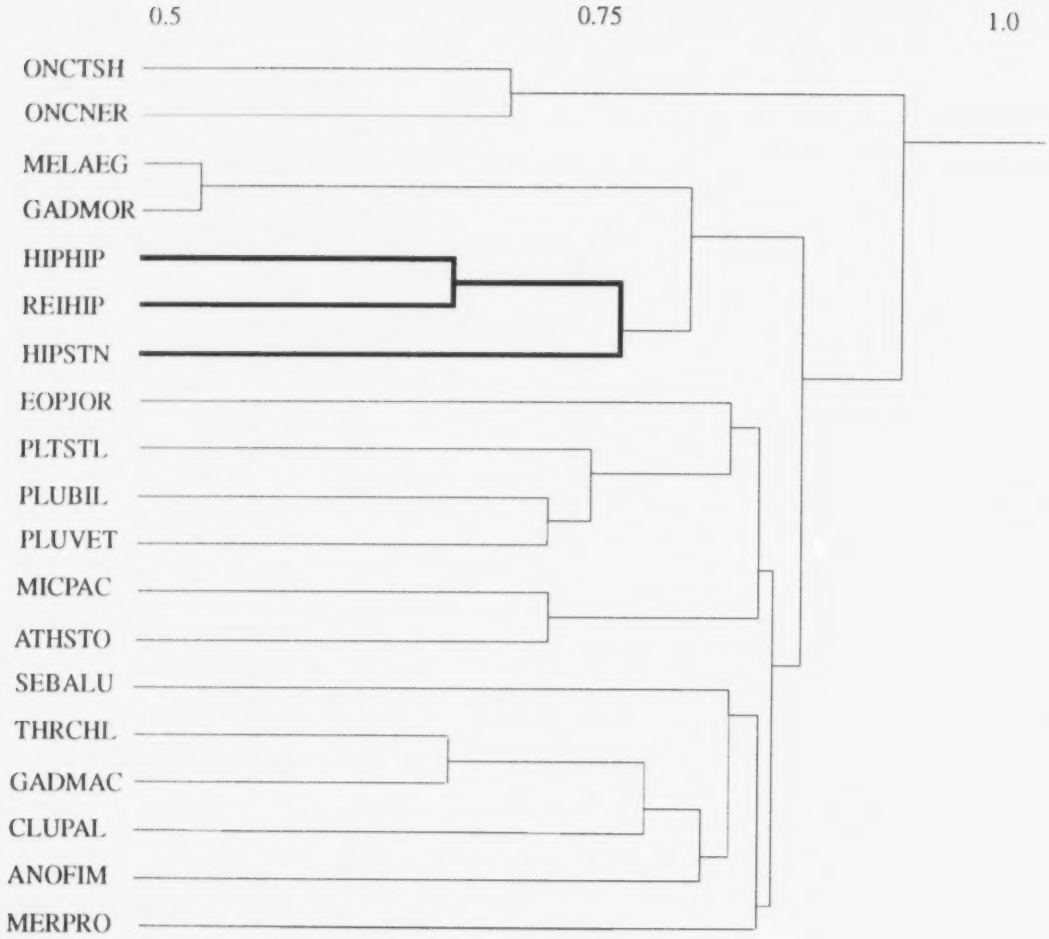

Figure 2.6. Cluster dendrogram of select Atlantic and Pacific fishes. Distance measure is Jaccard's coefficient, algorithm is average linkage. Halibut cluster is shown in bold. ATHSTO= *Atherestes stomias* (Arrowtooth flounder - Pacific), ANOFIM= *Anoplopoma fimbria* (sablefish - Pacific), CLUPAL = *Clupea pallasi* (Pacific herring - Pacific), EOPJOR = *Eopsetta jordani* (petrale sole - Pacific), GADMAC= *Gadus macrocephalus* (Pacific cod - Pacific), GADMOR= *Gadus morhua* (Atlantic cod - Atlantic), HIPHIP = *Hippoglossus hippoglossus* (Atlantic halibut - Atlantic), HIPSTN = *Hippoglossus stenolepis* (Pacific halibut - Pacific), MELAEG = *Melanogrammus aeglefinus* (haddock - Atlantic), MERPRO = *Merluccius productus* (Pacific hake - Pacific), MICPAC = *Microstomus pacificus* (Dover sole - Pacific), ONCNER = *Oncorhynchus nerka* (sockeye salmon - Pacific), ONCTSH = *Oncorhynchus tshawytscha* (chinook salmon - Pacific), PLTSTL = *Platichthys stellatus* (starry flounder - Pacific), PLUBIL - *Pleuronectes bilineatus* (rock sole - Pacific), PLUVET = *Pleuronectes vetulus* (English sole - Pacific), REIHIPP = *Reinhardtius hippoglossoides* (Greenland halibut - Atlantic and Pacific), SEBALU = *Sebastes alutus* (Pacific Ocean perch - Pacific), and THRCHL= *Theragra chalcogramma* (walleye pollock - Pacific).

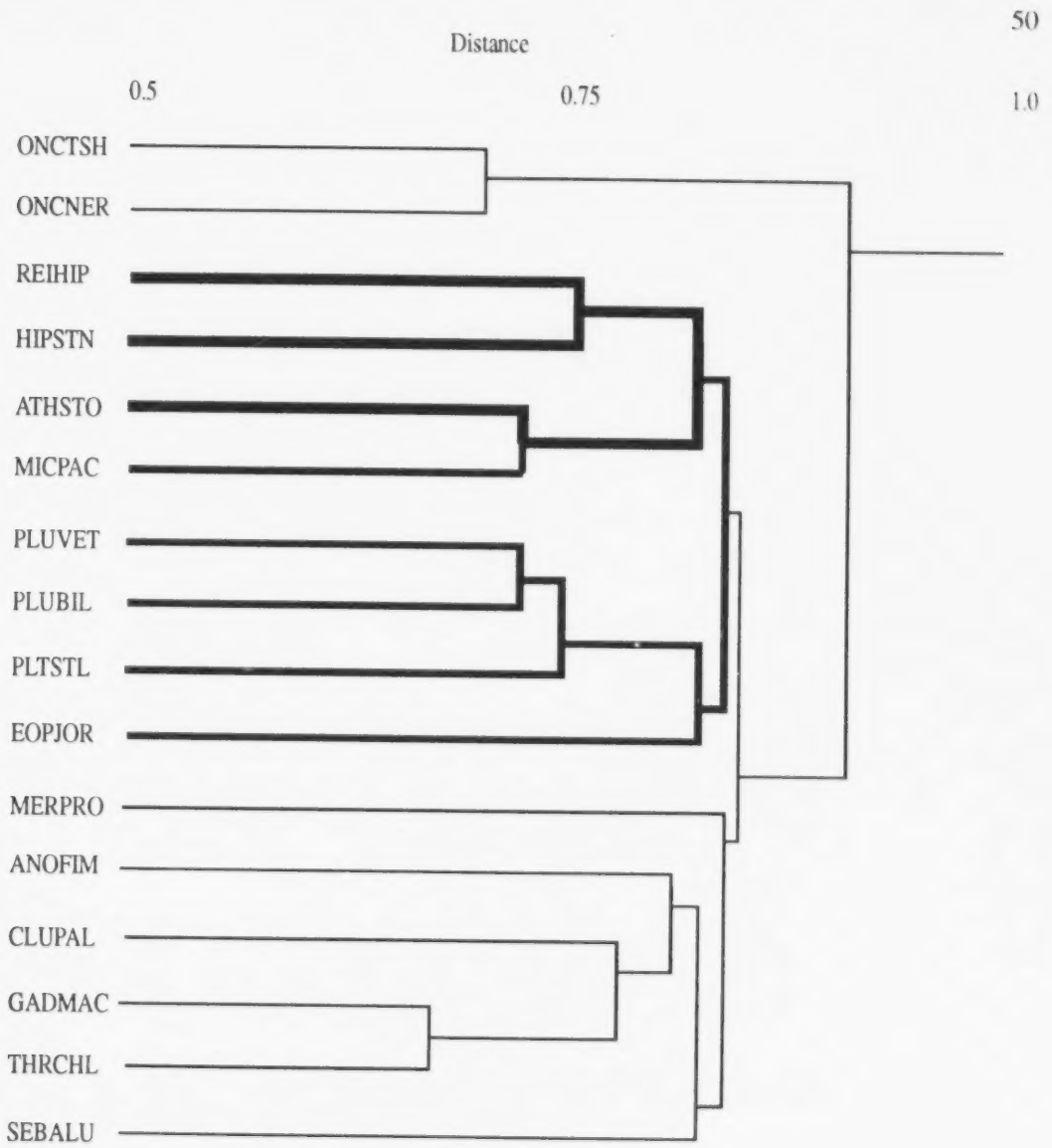

Figure 2.7. Cluster dendrogram for Pacific species. Distance measure is Jaccard's coefficient, algorithm is average linkage. Halibuts are shown in the boldest line. Other Pacific flatfishes are shown in intermediate thickness. Abbreviations are as in Figure 2.6.

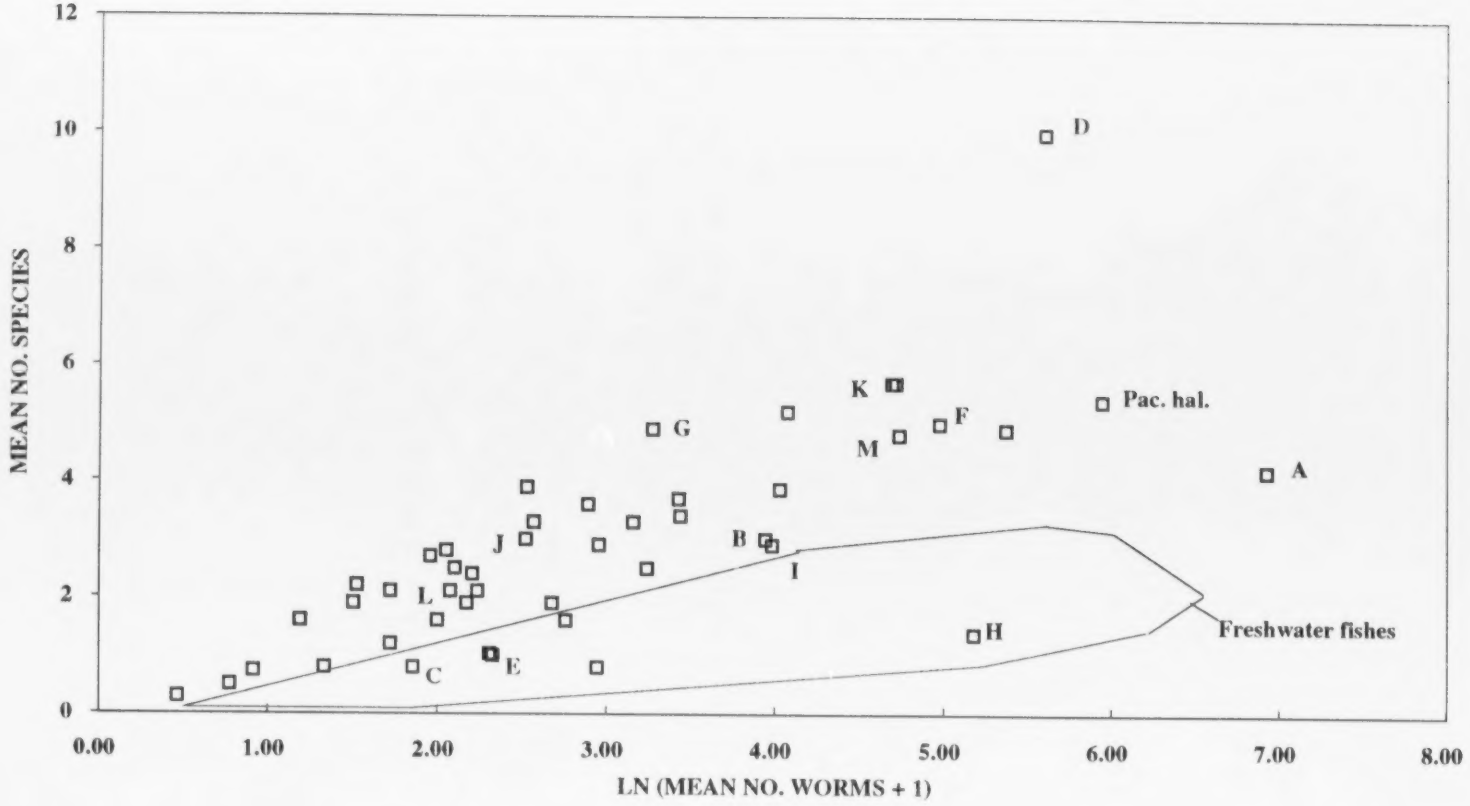

Figure 2.8. Community richness of gastrointestinal helminths of marine fishes. Pac. hal. represents Pacific halibut. The polygon represents the range of values for freshwater fishes. A = *Reinhardtius hippoglossoides*, B = *Hippoglossus hippoglossus*, C = *Atherestes stomias*, D = *Sebastes nebulosus*, E = *Anoplopoma fimbria*, F = *Sebastes paucispinis*, G = *Sebastes ruberrimus*, H = *Oncorhynchus tshawytscha*, I = *Oncorhynchus nerka*, J = *Sebastes alutus*, K = *Gadus morhua*, L = *Sebastes elongatus*, M = *Theragra chalcogramma*.

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CHAPTER 3 - ZOOGEOGRAPHY

The aim of zoogeography is to elucidate and explain large-scale geographic patterns in species distributions and abundances. One major focus has been on characterizing faunal zones, based mainly on their species compositions. Significant work in the second half of this century (Hedgepeth 1957; Briggs 1974) has led to a reasonably thorough delineation of marine faunal regions. Regions, which are often correlated with temperature and the adjacent major ocean currents, are characterized by distinct species assemblages and high levels of endemism, particularly of molluscs and fishes (Briggs 1974).

The eastern north Pacific is divided into the Arctic and Eastern Boreal Pacific (EBP) regions (Briggs 1974; NOAA 1990). The Arctic region covers the central and northern Bering Sea. This region is characterized by cold water (0-3.5°C) flowing in the counterclockwise Arctic Basin Gyre. Water enters the Bering Sea through the Aleutian chain and exits through the Bering Strait and along the Kamchatka Peninsula. There is significant ice cover in many regions. Endemism is high, but diversity is low (Dodimead et al. 1963; NOAA 1990). The EBP extends from southern California into the central Bering Sea where it joins the Arctic region. The EBP is characterized by warmer water (5-10°C) derived from the eastward flowing West Wind Drift and Kuroshio currents. Species diversity and endemism are high.

Within the EBP there are two provinces based on characteristic species assemblages and levels of endemism (NOAA 1990). The Aleutian Province spans the distance from northern Vancouver Island to the Bering Sea and is associated with the northern division of the West Wind Drift current, which divides as it approaches the Vancouver Island area. The current then forms the Alaskan Gyre which circulates in the Gulf of Alaska. Some water input is also received from the eastward flowing Subarctic Current (Dodimead et al. 1963; NOAA 1990). The Aleutian Province is sometimes divided into subareas based on topography. These subareas differ primarily in the relative abundances of species rather than the presence or absence of species (NOAA 1990). The Oregonian Province covers southern California to northern Vancouver Island and is associated with the southern division of the West Wind Drift (California Current). Water is slightly warmer than in the Alaskan Gyre (5-15°C) and, in the northern areas, is often mixed by upwelling from the deeper and warmer California Counter Current. There are two subareas in the Oregonian Province, based in part on the

upwelling patterns (Dodimead et al. 1963; NOAA 1990).

Zoogeographic studies have not usually included parasites, primarily because little is known about marine parasite distributions. Manter's studies (1940, 1947, 1955) were among the earliest attempts to examine zonation patterns in marine parasite distributions. He compared digenean species richness and overlap among different oceans and regions and found that as distance between sites increased, the degree of overlap decreased. Other studies have found similar patterns. Based on these studies, Lebedev (1969) established 10 oceanic regions based on the monogenean and digenean fauna. He recognized only two regions in the entire eastern North Pacific: the tropical eastern Pacific from 32°N to 10°S and the northeast Pacific region encompassing all the area to the north. Although Lebedev was concerned with broad scale, open water, pelagic fauna and did not consider coastal areas, his northeast Pacific region roughly corresponds to the Eastern Boreal Pacific.

Another major focus has been on the examination and explanation of latitudinal and depth gradients in species richness (see references in Rohde (1992)). Overall, species richness is inversely related to latitude (Kuznezov 1957; Schall and Pianka 1978; Ben Eliahu and Safriel 1982), although some taxa do not show this pattern (Janzen 1981; Rohde 1993). Rohde (1992) reviewed the various hypotheses explaining the latitudinal gradient and concluded that the usual arguments of increased competition and niche diversification, environmental stability and area, and ecological and evolutionary time were unsatisfactory explanations. He concluded that the explanation was related to greater evolutionary speed in the tropics as a result of increased energy (temperature). With respect to latitudinal gradients in parasite species richness, Monogenea show the typical richness trend, but the data for Digenea and marine mammal parasites are less clear (summarized in Rohde 1993). Latitudinal trends in abundance are less clear and more difficult to explain, though temperature may play an important role. Rohde (1977, 1981) found no relationship between abundance and latitude in the Monogenea.

Another focus has been on trends in diversity and abundance due to depth. Sanders (1969) and Rex (1981) found an increase in diversity with depth. Abele and Walters (1979) attributed differences to the species-area effect. Rohde (1992) hypothesized that the vast area of the deep sea along with its lack of disturbance would promote diversity. He also noted that this pattern may be mitigated by temperature

decreases. Studies on the effects of depth on parasites have shown that patterns are dependent upon the organism being examined. For benthic fishes, Heath (1987) and Campbell et. al. (1980) concluded that depth made little difference in the diversity or abundance of the parasite fauna (except for major decreases at abyssal depths). Campbell (1990) suggested that those fishes that migrate vertically have higher prevalences of nematode infection. Rohde (1988) found a negative relationship between depth and richness of the monogenean fauna.

The literature is replete with studies that look at parasites from a variety of fishes in disjunct localities (Manter's studies were of this type), but these types of studies may be biased due to the ecological and phylogenetic differences among hosts. Studies that examine the same host in different localities also are common, but they often do not have sufficient geographic coverage to permit conclusions beyond the local level. Few studies have examined widely distributed hosts over a significant portion of their range, in part because of the difficulty of collecting over such a wide geographic area. The Pacific halibut is an Arctic/Boreal Pacific species with its center of distribution in the Gulf of Alaska, but with significant numbers extending throughout the EBP (NOAA 1990), thus providing an excellent opportunity to examine parasite zonation and diversity gradients.

Therefore, in this chapter, I examine the parasite fauna of Pacific halibut over much of its North American range attempting to assess:

1) whether the parasite fauna of halibut in the eastern North Pacific shows a zoogeographic pattern,

2) if so, where the boundaries are,

3) how any such pattern compares with known zoogeographic patterns, and

4) whether parasites of halibut exhibit latitudinal and depth gradients.

MATERIALS AND METHODS

This chapter focuses on the parasites of the 336 adults (>55 cm fork length) from 15 geographic localities (Fig. 3.1, Table 3.1). Fish were caught by longline and trawls, individually tagged and bagged with depth and locality information, and immediately deep frozen by the staffs of the International Pacific Halibut Commission (IPHC) and the U.S. National Marine Fisheries Service for later examination. Sampling localities and regions were established based on a combination of management zones recognized by the IPHC, the existing knowledge of zoogeographic zonation in the North Pacific, and convenience. My study area lies primarily in the Aleutian Province of the EBP Region. One locality (St. Matthew Island) in the northern Bering Sea lies in the border area between the Arctic and EBP regions. Three southern localities (Oregon, Washington, and Vancouver Island) lie in the Oregonian Province of the EBP.

Procedures for processing fish and parasites are detailed in Chapter 2.

Zoogeographic groupings were initially determined by examining the data for patterns of parasite presence and commonness. Parasites in each locality were classified into categories: 1) Very common (present in > 60% of the sample), 2) Common (present in 40-60% of the sample), 3) Moderate (present in 25 - < 40% of the sample, 4) Sparse (present in ≥ 10 - < 25% of the sample), and 5) Rare (present in < 10% of the sample). Patterns suggested by this analysis were clarified by cluster analyses using average linkage of 1) individual hosts using $\log_{10}$ (n+1) transformed intensity data and Euclidean distance and 2) localities using A) prevalences of each parasite species per locality and Euclidean Distance, B) the average number of worms of each species per locality and Euclidean Distance, and C) percentage similarities based on each species' proportion of the average worm number per locality. These analyses were repeated with systematic exclusion of: 1) parasites present everywhere at similar levels of infection (coded A in Appendix 1), 2) parasites discontinuous (spotty pattern of presence or prevalence) in distribution (coded B in Appendix 1), and 3) rare (present in <5 fish) and discontinuous parasites (coded C in Appendix 1). Variation in such species can be considered noise in the system that obscures zoogeographic pattern. In addition, I analyzed random similarities within hauls, localities, and regions using Jaccard's coefficient and percent similarity measures (in the percentage similarity analysis, those parasites that were of high and roughly equal intensities everywhere and those that were discontinuous in intensity patterns were excluded from the analysis). For analyses

requiring numbers of individuals, myxosporeans, recorded only as present, were assigned the value of the average number of worms per species in that fish. In this procedure, a fish was randomly drawn from a sample (haul, locality, or region). A second fish was randomly drawn from the same sample and similarity between the two was determined. Then, a third fish was randomly drawn from outside that sample and similarity with the first fish determined. Thirty groups of fish were drawn and mean similarity values within and across groups were calculated. This procedure was repeated 1000 times and mean within group similarity values were compared to mean across group similarity values. In analyses using regions, the definition of region was varied to maximize within region similarities and minimize across region similarities.

The effect of depth and latitude on the parasite fauna was investigated using standard regression with partial correlations, controlling for fish length. To avoid possible intercorrelations among zoogeography and depth, the three regions were analyzed separately. In the analysis for latitudinal trends, general patterns also were examined by plotting species richness (total number of taxa) and parasite mean abundance versus locality.

I follow the definitions of Margolis et al. (1982) for prevalence, abundance, and intensity.

RESULTS

Many parasites of halibut are present throughout its North American range and others are distributed sporadically. There is a suite of species regularly found in high abundances everywhere (coded A in Appendix 1), a suite of species widespread in distribution, but abundant in only a few widely scattered localities (coded B in Appendix 1), and a suite of rare species (coded C in Appendix 1). The prevalence patterns of the other species, those that appear to be more common in contiguous localities (coded D in Appendix 1) suggests a general north/south cline of species (Table 3.2 and Appendix 1). There are no consistent breakpoints, suggesting that each species has independent boundaries. However, there do appear to be five subgroups of these species: species more common in southern localities (the first group in Table 3.2), species more commonly found in southern and central localities (the second group in Table 3.2), species characteristic of central localities (group three in Table 3.2), species common in central and northern localities (group four in Table 3.2), and species that are largely limited to northern localities (group five in Table 3.2). This pattern suggests three broad regions with indistinct boundaries defined by a group of species found primarily in each region plus two groups of species spanning the two contiguous regions.

Clustering of data summed within localities provides some clarification of the boundaries. Clustering based on prevalences (Figure 3.2) indicates that Oregon and Washington localities group, Vancouver Island through Southeast Alaska 2 localities group, and Kodiak Island through St. Matthew Island localities group (although the St. Matthew Island locality appears to be somewhat isolated within this group). The Kenai Peninsula locality is isolated. Clustering based on parasite numbers using percentage similarity (Figure 3.3) suggests two main groups, an Oregon - southeast Alaska 1 group and a Kodiak Island - Pribilof Island group (including southeast Alaska 2), with the Kenai Peninsula, Nagai Island, and St. Matthew Island isolated. Using Euclidean Distance on the average numbers of each parasite species in each locality (not shown), clustering is markedly affected by abundances. Areas with high average abundances are isolated. If the widespread, exceptionally common and rare species are excluded from the analysis (Figure 3.4), the results roughly correspond to the results of the cluster based on prevalences. The major exception is that the southern Queen Charlotte locality and the southeast Alaska 2 locality are grouped and then joined to the northern group. St. Matthew Island is an integral part of the northern group. The combination of these analyses provide support

for an Oregon/Washington group and reasonably strong support for a northern group comprised of Kodiak Island through at least the Pribilof Islands. There is equivocal support for a central group, but that group is variable. The Kenai Peninsula group appears to be isolated in both analyses, but the St. Matthew Island group is isolated only in the analysis using percent similarity.

Random similarity analysis showed that measures of within group similarity were consistently higher than across group similarity (Table 3.3), indicating that there are patterns within groups of contiguous localities. In all cases, variances were extremely low (10^{-3} or 10^{-4}), indicating that small changes in mean similarity are significant. The best two-region grouping (Oregon through southeast Alaska 1 and southeast Alaska 2 through St. Matthew Island) had significantly lower within group similarities than the best three-region grouping (Oregon through the southern Queen Charlottes, the northern Queen Charlottes through Kenai Peninsula, and Kodiak Island through St. Matthew Island) and the best four-region grouping (Oregon through the northern Queen Charlottes, southeast Alaska 1 through southeast Alaska 2, Kenai Peninsula through Unimak Pass, and the western Aleutian Islands through St. Matthew Island). The latter two differed primarily in the lower between group similarities of the three-region grouping. The best fit indicated a southern group including localities from Oregon through the southern Queen Charlottes, a central group consisting of localities from the northern Queen Charlottes through the Kenai Peninsula, and a northern group consisting of localities from Kodiak Island north.

Cluster analyses of individual fish (Table 3.4 and Figure 3.5) was influenced by an overall similarity in the data. For example, cluster 19 contains fish from almost every locality. Neighboring localities often grouped at low levels, but there was no grouping pattern at higher levels. The zoogeographic divisions derived in the previous analyses were largely supported in this analysis. The Oregon - southern Queen Charlotte grouping is supported by clusters 2, 14, 16, and 23 (the Oregon/Washington group is supported only by clusters 2 and 12). The northern Queen Charlottes through Kenai Peninsula grouping is supported by clusters 5, 6, and 20. A Kodiak Island through the Bering Sea grouping is supported by clusters 3, 9, 11, and 15, although clusters 13 and 17 suggest that the St. Matthew Island locality may be distinct in that these two clusters contain 89% of the St. Matthew Island fish. Note that 62% (62/100) of the fish from southern localities are in clusters supporting that grouping (in bold in Table 3.4), and 63% (99/158) northern fish are in

the northern clusters, but only 27% (21/79) central fish are in the central clusters. Moreover, only 2 northern fish clustered with the southern groups and only 4 southern fish clustered with the northern groups.

Latitude

The general pattern in species richness (average number of taxa) showed a peak in the Gulf of Alaska and declines in both more northern and more southern localities, with lowest values in Vancouver Island, southern Queen Charlotte Island, and Nagai Island localities (Figure 3.6). The general pattern in mean abundance of parasites showed a peak in the south, declining northward, with a slight rise in the southern Bering Sea (Figure 3.7). Lowest values were in the Kenai Peninsula, Kodiak Island, and St. Matthew Island localities (see Chapter 5 for a more detailed statistical analysis). Overall, the number of species is positively related to latitude ($p < 0.001$, $r^2 = 0.039$), although the explained variance is very low and the variability in the data increases with latitude (Figure 3.8). The number of parasites is negatively related to latitude (Figure 3.9) ($p < 0.001$, $r^2 = 0.190$). When fish length is controlled, species number remains positively related to latitude ($p = 0.001$, $r_p = 0.198$) and the relationship between parasite number and latitude is still negative ($p = 0.001$, $r_p = -0.438$) as well.

Depth

Larger fish often inhabit greater depths, therefore, length was controlled in the depth analysis. Overall, fish taken from greater depths had more species ($r_p = 0.342$, $p < 0.001$), but fewer parasites ($r_p = -0.270$, $p < 0.001$); although these relationships were significant, they explained relatively little of the variance in infracommunities. In the southern region, both species number ($r_p = -0.252$, $p = \sim 0.04$) and parasite number ($r_p = -0.268$, $p = \sim 0.03$) were negatively correlated with depth. In the central region, species number was positively correlated with depth ($r_p = 0.373$, $p < 0.001$), but the number of parasites was negatively correlated ($r_p = -0.212$, $p = \sim 0.02$). In the northern region, species number was positively correlated with depth ($r_p = 0.313$, $p < 0.001$), but the number of parasites was not ($r_p = 0.014$, $p > 0.5$)

DISCUSSION

My analyses demonstrate much similarity in the parasite fauna of Pacific halibut throughout the northeast Pacific. Many species were found throughout the study area. None of the abundant parasites were considered endemic to any particular region, especially when records from other fishes are considered. The patterns I have identified are primarily due to differences in prevalence and/or abundance. That these patterns become much clearer when the noise provided by the ubiquitous and discontinuous species are excluded from the analyses, further emphasizes the overall similarity in the parasite fauna.

The clearest pattern I have identified is an overall clinal variation in parasite infracommunities, with the clearest distinction between fish from northern and southern localities. This is shown particularly well by the cluster analyses of individual fish. Over 60% of northern fish are in clusters dominated by northern fish and very few northern fish join clusters dominated by southern fish. The equivalent pattern was seen in southern fish. Fish from central localities often have species with both northern and southern affinities. There are many parasite species that are present primarily in either southern and central regions or in central and northern regions. Thus, the fauna of the central region is a mixture of northern and southern faunas with a few unique characteristics. Again, this is seen in the cluster of individual fish, where only 27% of the central fish cluster together, and larger numbers of central fish join northern and southern groups.

However, all analyses suggest that there are breaks in the otherwise continuous variation. Clustering of localities using percent similarity suggests a two region grouping, with localities south of the southeast Alaska 2 locality forming the southern group and localities north forming the northern group. However, none of the other analyses support this grouping. Clustering of localities using prevalences suggests a division in or near the Bering Sea, but again, none of the other analyses support such a grouping. Several lines of evidence support the existence of 3 regions. Prevalence patterns show that the three regions have species that are concentrated in that region. Cluster analyses of data summed within localities clearly show that contiguous localities in southern, central and northern regions group together, particularly after exceptionally common and rare species are removed. The random similarity analysis indicates maximum within-region similarity and minimum across-region similarity with a three region grouping.

These analyses suggest that the southern breakpoint lies around the Queen Charlotte Islands. The

strongest evidence comes from the random similarity analysis, which clearly indicates that, with the northern boundary held constant, using the southern Queen Charlottes as the breakpoint for the southern region dramatically increases within region similarity. Additional support comes from clustering of individual fish, in which those clusters that are predominantly southern fish usually contain fish ranging from Oregon to the southern Queen Charlotte Islands. Although clustering of data summed within localities sometimes suggests a Washington/Vancouver Island boundary, this boundary is not supported by any other analyses. The grouping of Washington and Oregon may be driven by the abundance of parasites in combination with the slightly higher number of species compared to immediately adjacent localities.

The northern breakpoint occurs southeast of Kodiak Island. Again the strongest evidence comes from the random similarity analysis, which demonstrates that changing this boundary reduces within-group similarity. As well, in the cluster of individuals, those clusters that contain largely northern fish most often contain fish ranging from Kodiak Island north. All three clusters of localities suggest a boundary south of Kodiak Island.

Although the similarity analysis places the Kenai Peninsula locality in the central group, this locality does not group with anything in any of the cluster analyses. Even the majority of the individual fish cluster separately (group 4 in Table 3.4). An examination of the data from the Kenai Peninsula locality reveals a suite of several very common species that are more consistently common than in surrounding localities. The suite of species includes *Scolex pleuronectis* (intestine), *S. pleuronectis* (gall bladder), *Podocotyle gibbonsia*, and *Contracaecum* sp. In addition, the intensity of *Capillaria margolisi* in the Kenai locality is exceptionally high compared to surrounding localities, thus possibly serving as an additional distinguishing factor for this locality.

My data also suggest that the northernmost locality (St. Matthew Island), although still quite similar to the other northern localities, is less similar to them than the other northern localities are among themselves. In the cluster of individuals, the locality is distinct as well, with over half the fish from this locality occupying a single cluster and almost 90% of them occupying two clusters. Species richness is approximately the same as surrounding areas, but the overall abundance of parasites decreases in this locality. It appears that this decrease is largely due to decreased numbers of two of the dominant species, *Tubulovesicula lindbergi* and

Anisakis simplex. Its proximity to the Arctic zone may suggest a transition to Arctic fauna.

The zoogeographic boundaries I observed roughly correspond to the divisions previously identified for the eastern North Pacific, especially for the southern region. Various observers have placed the southern boundary at various points between Puget Sound and Dixon Entrance. Briggs (1974) placed it at Dixon Entrance (near my northern Queen Charlotte Island sample). NOAA (1990) suggested northern Vancouver Island. My data on halibut parasites suggest a boundary between those suggested by Briggs and NOAA.

Briggs (1974) and NOAA (1990) agreed that the Bering Sea has some unique characteristics, but both considered at least part of it as part of the Aleutian Province. Briggs (1974) did not discuss subdivisions. NOAA (1990) recognized a subdivision in the vicinity of Unimak Pass, with everything south of the Aleutian Islands separate from the Bering Sea. My data suggest that both the Bering Sea and the surrounding Aleutian Islands have characteristics that separate them from central areas as a single group (again with some vagueness to the boundaries). However, my data do not support a major faunal break in this region (see Chapter 4).

Most of the known zoogeographic patterns have been established through examination of invertebrate fauna, particularly molluscs. Because many parasites are dependent upon molluscs (digeneans) and other invertebrates (nematodes, cestodes, acanthocephalans), I would expect the zoogeographic zonation of parasites to correspond to that of the various invertebrates. Because the complex life cycles of parasites often involve more than one (often mobile) intermediate host, each of which may have different distributions, the vagueness in the boundaries between zones is not unexpected.

Some of the overlap may also be due to fish movement; thus, overlap may give us an idea of the extent of movement. It appears that large scale movements are not common or at least not fast. Fish remain in a region long enough to develop its characteristic fauna. GI helminths, several of which were used to help establish pattern, probably are lost fairly quickly after a fish leaves the transmission area. The data also give us an indication of the direction of movement. Bering Sea parasite species are rarely seen far outside the Bering Sea and some species found virtually everywhere else are rarely found in the Bering Sea, suggesting that migration in or out of the Bering Sea is limited. The oceanographic or geologic conditions around the Aleutian Islands may act as a barrier to significant migration. Further, the drift of larvae into the Bering Sea and the spawning grounds within the Bering Sea may serve to maintain the population without significant immigration

or emigration. Southern fish appear to move north more readily than central fish move south as shown by the commonness of some southern species as far north as southeast Alaska. Spawning migrations and current might be expected to bring southern fish north. Fish from the Gulf of Alaska appear to move the least because there are species limited primarily to the Gulf of Alaska area. The center of halibut distribution and spawning is in the Gulf of Alaska and thus many fish may be expected to remain in the area.

Depth

The general pattern with respect to depth is a positive relationship with parasite species number and a negative relationship with parasite number. There are two exceptions to this pattern: 1) a negative relationship with species number in the south, and 2) no relationship with parasite number in the north. Elucidating these patterns and determining their cause or causes are difficult for at least two reasons. First, the collection methods were such that only average depths could be assigned to hauls that may have included fish from very different depths. Second, halibut have a wide depth distribution and actively feed throughout the water column (Hart 1973; NOAA 1990). Therefore, the depth at which a halibut is caught is not necessarily indicative of the depth at which the animal was living. Nevertheless, the general pattern may be instructive. Temperature may be driving the negative relationship between parasite number and depth. Fish that live at greater depths exist in a colder environment, thus digestion is slower and food intake (thus exposure to parasites) would be lower than at a higher temperature (shallower depth). The positive relationship between depth and species number may be related to feeding range. Halibut feed throughout much of the water column; therefore, halibut living at greater depths may cover more area during feeding and be exposed to more species of parasites. The negative relationship between species number and depth in the south may be related to the narrower continental shelf in the south. A narrower continental shelf may provide less habitat from which halibut can acquire parasites. The lack of correlation between parasite number and depth in the north may be related to the lower overall temperature and the narrower temperature ranges in the north.

Latitude

Latitudinal gradients in species richness are well known in parasites (Rohde 1992) as well as freeliving organisms (Pianka 1966). Generally, species richness increases toward the equator, presumably because of greater evolutionary rates in tropical areas (Rohde 1992). My data do not support the idea of an increase in species richness toward the equator. Rather, the number of species (and the variability in species number) increases with latitude. Species richness appears to be correlated with halibut abundance (see Chapter 5). The central region is the center of halibut abundance, with some decrease in abundance to the north, but more significant decreases to the south (NOAA 1990; Sullivan and Parma 1995). In an area of high abundance, halibut may expand their niche and/or diet. In doing so, they may be exposed to a wider variety of parasites. In addition, the increase in variability suggests that local geographic factors rather than latitudinal factors are creating the pattern. Pianka (1966) and Brown and Gibson (1983) recognized the influence of physical heterogeneity in shaping the fauna of a particular region. Large populations of halibut also may facilitate efficient cycling of parasites. Because halibut do have a richer and more abundant fauna than most marine fishes, halibut may play a significant role in maintaining some parasite populations.

Rohde (1981) found no patterns in the abundance of Monogenea in relation to latitude. My data show a definite trend. Parasite abundance is greatest in the south. Leaman and Kabata (1987) found a similar pattern for a copepod that requires no intermediate host and suggested that temperature may play a role (though not the primary role) in producing the pattern. Indeed, Rohde (1992) concluded that temperature was an important factor in producing latitudinal gradients. As temperature increases, the rate of digestion increases; therefore, fish probably eat more, grow faster, and get more parasites.

The increase in abundance in the Bering Sea is interesting. The most likely explanation for this pattern is probably geological. The Bering Sea is a broad, shallow, highly productive basin (Briggs 1974). This may result in a richer, more abundant community through which parasites may cycle, but the increase may be mitigated by the increasing harshness of the environment in higher latitudes.

Summary

I have shown overall clinal variation in parasites of Pacific halibut in the northeast Pacific with respect to the distribution of parasites, latitude, and depth. However, I also have shown patterns within this clinal variation. I have shown evidence of three zoogeographic regions with parasite species characteristic of each. Southern fish are distinctive due to the increased abundance of parasites. Central fish are distinctive due to a greater number of species, which is due, in part, to the clinal variation, but may also be related to halibut abundance. Northernmost fish are distinctive due to decreased parasite abundance. Whether the depth and latitude patterns are the cause of or the result of these zoogeographic patterns is still unclear.

Table 3.1. Collection data for samples of adult and juvenile Pacific halibut, *Hippoglossus stenolepis*.

Locality	Haul	n	Lat/Long (range for composites)	$\bar{x}$ depth (ranges of means for composites) (m)	Collection date
ADULTS					
OR	1*	3	40.53N 124.25W-41.15N 124.25W	125.3 (125-126)	24-25 Aug 92
	2*	6	42.15N 124.29W-43.06N124.29W	63.5 (38-133)	28-31 Aug 92
	3*	4	44.15N 124.21W-44.55N 124.43W	56 (47-65)	2 Sep 92
	OR*	10	44.55N 124.11W-45.35N 124.29W	109.7 (56-123)	7 Sep 92
WA	WA*	10	46.24N 124.29W-47.35N124.02W	97.2 (48-108)	11-16 Sep 92
	1*	2	46.00N 124.28W-46.14N 124.24W	92.8 (76-131)	8-10 Sep 92
	2	2	47.45N 125.02W	91 (81-101)	17 Sep 92
VI	VI	12	48.17N 125.32W	128	24 Jul 90, 14 Sep 91
	1*	20	47.45N125.01W-48.20N 125.33W	93.3 (74-130)	14 Sep 91, 17 Sep-1 Oct 92
SQC	SQC	31	52.22N 130.57W	136	15 Jun 91
NQC	1*	8	54.28N 133.56W-55.20N 134.43W	323.8 (304-332)	5 Sep 92
SA1	1	6	55.57N 135.24W-56.50N 136.00W	295.6 (293-297)	28-30 Aug 92
	SA1*	10	57.11N 136.15W-57.30N 136.30W	314.7 (312-321)	28-30 Aug 92
	2	4	58.08N 138.43W	295	26 Aug 92
SA2	SA2	15	59.31N 144.42W	287	19 Aug 92
	1	15	59.34N 143.37W	293	20 Aug 92
KP	KP	21	57.59N 149.09W	296	9 Aug 92
KI	2	11	57.07N 151.16W	287 (286-290)	6 Aug 92
	1	3	56.00N 154.37W-56.18N 153.01W	278.6 (246-344)	3 Aug 92
	KI*	12	56.00N 154.01W	249	3 Aug 92
NI	NI	14	54.31N 159.10W	120	27 Jul 92

Table 3.1(continued).

Locality	Haul	n	Lat/Long (range for composites)	$\bar{x}$ depth (range of means for composites) (m)	Collection date
UP	1	11	54.08N 161.38W	173	24 Jul 92
	2	9	53.44N 164.22W	243	22 Jul 92
WAI	1	1	52.59N 167.40W	232	19 Jul 92
	WAI	20	52.40N 169.01W	228	18 Jul 92
SB	SB	20	53.02N 170.08W	265	1 Jun 92
	1	6	53.35N 168.16W	263	2 Jun 92
	2	4	54.06N 166.23W	265	3 Jun 92
	3	1	54.55N 166.12W	90	4 Jun 92
PI	PI*	11	56.03N 169.38W-58.46N 177.34W	179.5 (88-280)	9-16 Jun 92
	1*	3	59.20N 178.17W-59.48N 178.43W	183 (131-249)	18-24 Jun 92
SMI	1*	9	60.06N 178.51W-60.07N 178.52W	198	21 Jun 92
	2*	12	60.19N 178.22W-60.30N 178.18W	107.7 (101-109)	20-22 Jun 92
	SMI	10	60.50N 178.18W	96	19 Jun 92
JUVENILES					
NQC		20	54.16N 131.32W	73	7 Sep 90
KI		13	56.21N 154.31W-58.38N 153.30W	29.7 (10.64)	17 Jul 90-21 Jun 94
NI		20	55.12N 157.26W-55.53N 157.00W	97 (82-118)	4-29 Jul 90
UP		20	54.15N 161.42W-54.53N 160.27W	78.5 (73-84)	22-23 Jun 90
PI		23	59.20N 165.56W-59.39N 165.57W	22	27-28 Jun 91

* = composite haul

OR - California and Oregon
WA - Washington
VI - Vancouver Island
SQC - Southern Queen Charlottes
NQC - Northern Queen Charlottes
SA1 - Southeast Alaska
SA2 - Southeast Alaska 2
KP - Kenai Peninsula
KI - Kodiak Island
NI - Nagai Island
UP - Unimak Pass
WAI - Western Aleutian Islands
SB - Southern Bering Sea
PI - Pribilof Island
SMI - St. Matthew Island

Table 3.2. Prevalence patterns of species showing a geographic gradient. Data based on 432 juveniles and adults. Vertical lines indicate final zoogeographic regions. Abbreviations as in Table 3.1.

	Geographic locality														
Parasite	OR	WA	VI	SQC	NQC	SA1	SA2	KP	KI	NI	UP	WAI	SB	PI	SMI
SOUTHERN SPECIES															
Cucullanus heterochrous	++	++	+	+	-	-	+	-	+	+	+	+	-	-	+
Spirurid gen. sp.	++	C	+	-	-	++	+	+	+	-	+	-	+	-	-
Leptotheca sp.	+	++	+	+	-	+	-	-	-	-	-	-	-	-	-
Paracapillaria parophrysi	V	V	++	+	+	C	++	+	-	+	+	+	++	-	-
SOUTHERN AND CENTRAL SPECIES															
Otodistomum sp.	C	+++	+	+++	++	+++	++	++	+	+	-	+	-	-	+
Prosorhynchoides basargani	V	V	V	+	C	++	C	+	-	-	+	+	+	+++	+
Scolex pleuronectis (int)	V	C	V	V	V	C	+++	V	C	+++	++	++	+++	++	++
Scolex pleuronectis (gb)	+++	+++	+++	-	++	C	C	V	+++	+++	+	+++	+	-	-
CENTRAL SPECIES															
Lecithaster gibbosus	+	-	++	+++	-	+	++	+++	+	++	-	+	+	-	+
Podocotyle gibbonsia	-	-	+	+	V	-	++	V	+	+	+	-	-	-	-
Bolbosoma sp.	-	-	-	-	-	+	++	++	+	-	-	-	-	-	-
Corynosoma enhydri	-	-	-	-	-	-	+	+	+	-	+	-	-	-	-
Capillaria margolisi	+	-	+	+	-	-	++	++	++	-	+	+	+	-	-
Kudoa thyrsites	++	-	+	-	++	-	+	+	+	+++	++	-	-	-	-

Table 3.2 (continued).

Parasite	Geographic locality														
	OR	WA	VI	SQC	NQC	SA1	SA2	KP	KI	NI	UP	WAI	SB	PI	SMI
CENTRAL AND NORTHERN SPECIES															
Contracaecum sp.	-	-	+	-	++	+++	C	V	+++	+	+	+++	C	+	+
Nybelinia surmenicola	++	++	++	+	++	+++	C	C	C	++	+++	+++	C	+++	V
Echinorhynchus gadi	++	+++	+++	C	++	++	+++	V	C	C	C	V	C	+++	C
Steganoderma formosum	+++	+++	++	++	+	++	++	+	+++	+++	C	V	+++	C	C
NORTHERN SPECIES															
Genolinea laticauda	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-
Dissosaccus laevis	-	-	-	-	-	-	+	-	+	-	+	-	+	+	+
Podocotyle sinussacca	-	-	-	-	-	+	+	-	+	-	+	+	-	-	+
Hirudinoidea	-	-	-	-	-	-	-	-	-	-	+	-	+	-	++
Parahemiurus merus	-	-	-	-	-	+	-	-	-	+	-	-	+	++	+
Gonocerca phycidis	-	-	-	-	-	-	+	-	+	-	-	+	++	+	+
Bucephalid metacercariae	-	-	-	-	-	-	+	+	-	-	-	++	+	++	++

V = Very common (present in >60% of sample), C = Common (present in 40-60% of sample), +++ = Present in 25- < 40% of sample, ++ = Present in ≥ 10- < 25% of sample, + = Present in <10% of sample, - = absent

Table 3.3. Mean similarities within and across groups. Abbreviations for localities as in Table 3.1. Groups include all intervening localities and are separated by slashes.

Grouping (no. of groups)	Mean Similarity			
	Percent similarity/Variance (excluding widespread common and discontinuous species)		Jaccard's coefficient/Variance	
	Within	Across	Within	Across
Region (2)				
OR - NQC/SA1 - SMI	0.432/0.003	0.388/0.003	0.394/0.0005	0.358/0.0001
OR - SQC/NQC-SMI	0.426/0.003	0.398/0.003	0.393/0.0005	0.355/0.0004
OR - KP/KI - SMI	0.435/0.003	0.390/0.003	0.397/0.0004	0.354/0.0004
OR - SA1/SA2-SMI	0.437/0.003	0.384/0.003	0.397/0.0004	0.354/0.0003
Region (3)				
OR - SQC/NQC -KP/KI - SMI	0.458/0.003	0.390/0.003	0.408/0.0004	0.352/0.0003
OR - VI/SQC - KP/ KI - SMI	0.446/0.003	0.399/0.003	0.408/0.0005	0.355/0.0004
OR - SQC/NQC -KI/NI - SMI	0.442/0.003	0.388/0.003	0.411/0.0005	0.360/0.0003
OR - WA/VI - KP/KI - SMI	0.436/0.002	0.389/0.003	0.406/0.0004	0.353/0.0003
OR - WA/VI - SA2/KP - SMI	0.437/0.003	0.386/0.003	0.404/0.0004	0.353/0.0003
OR - NQC/SA1 - SA2/KP - SMI	0.440/0.003	0.388/0.003	0.403/0.0005	0.356/0.0004
OR - NQC/SA1- KP/KI - SMI	0.444/0.003	0.384/0.003	0.407/0.0004	0.355/0.0006
Region (4)				
OR - NQC/SA1 - SA2/KP - UP/ WAI - SMI	0.457/0.003	0.391/0.003	0.411/0.0005	0.359/0.0003
OR - SQC/NQC - KI/NI - AI/ SB - SMI	0.454/0.003	0.391/0.003	0.409/0.0005	0.359/0.0004
OR - SQC/NQC - KP/KI - UP/ WAI - SMI	0.453/0.003	0.390/0.003	0.412/0.0005	0.361/0.0004

Table 3.4. Cluster membership for clusters of individual fish from Figure 3.5. Vertical lines indicate final zoogeographic groupings. Joining distance indicates distance at which cluster is complete. Numbers in bold identify clusters associated with southern, central, or northern regions.

Cluster	Joining	Locality														
	distance	OR	WA	VI	SQC	NQC	SA1	SA2	KP	KI	NI	UP	WAI	SB	PI	SMI
1	1.079			3			2									
2	0.957	**9**	**5**	**1**			3									
3	1.031										**1**				**1**	**2**
4	1.041								12	2						
5	0.896						**1**	**4**								
6	0.966	1					**1**	**2**								
7	0.853					1	1			1			1	1	1	
8	0.750			2										1		
9	0.758			1										3	1	
10	0.568	**2**														
11	0.727						1	2		**1**		**2**	**1**	**7**	**1**	
12	0.803	**3**	**1**													
13	0.917		1											**1**	**2**	**17**
14	0.939	**2**			**2**											
15	0.835	1			1			1	6	**3**	**6**	**10**	**10**	**6**	**3**	**1**
16	0.750		**2**	**2**	**1**			1		1				1		

Table 3.4 (continued).

Cluster	Joining	Locality													
	distance	OR	WA	VI	SQC	NQC	SA1	SA2	KP	KI	NI	UP	WAI	SB	PI	SMI
17	0.742													**1**	**2**	**7**
18	0.706				5					**5**	**2**	**2**	**2**	**1**	**2**	
19	0.723		6		9	2	3	6	1	8	1	6	4	5	1	
20	0.737						**5**	**5**	**2**							
21	0.724								**1**	**2**						
22	0.801							4						1		
23	0.859	**1**	**15**	**3**	**13**	4	3									
24	0.882						1				1					

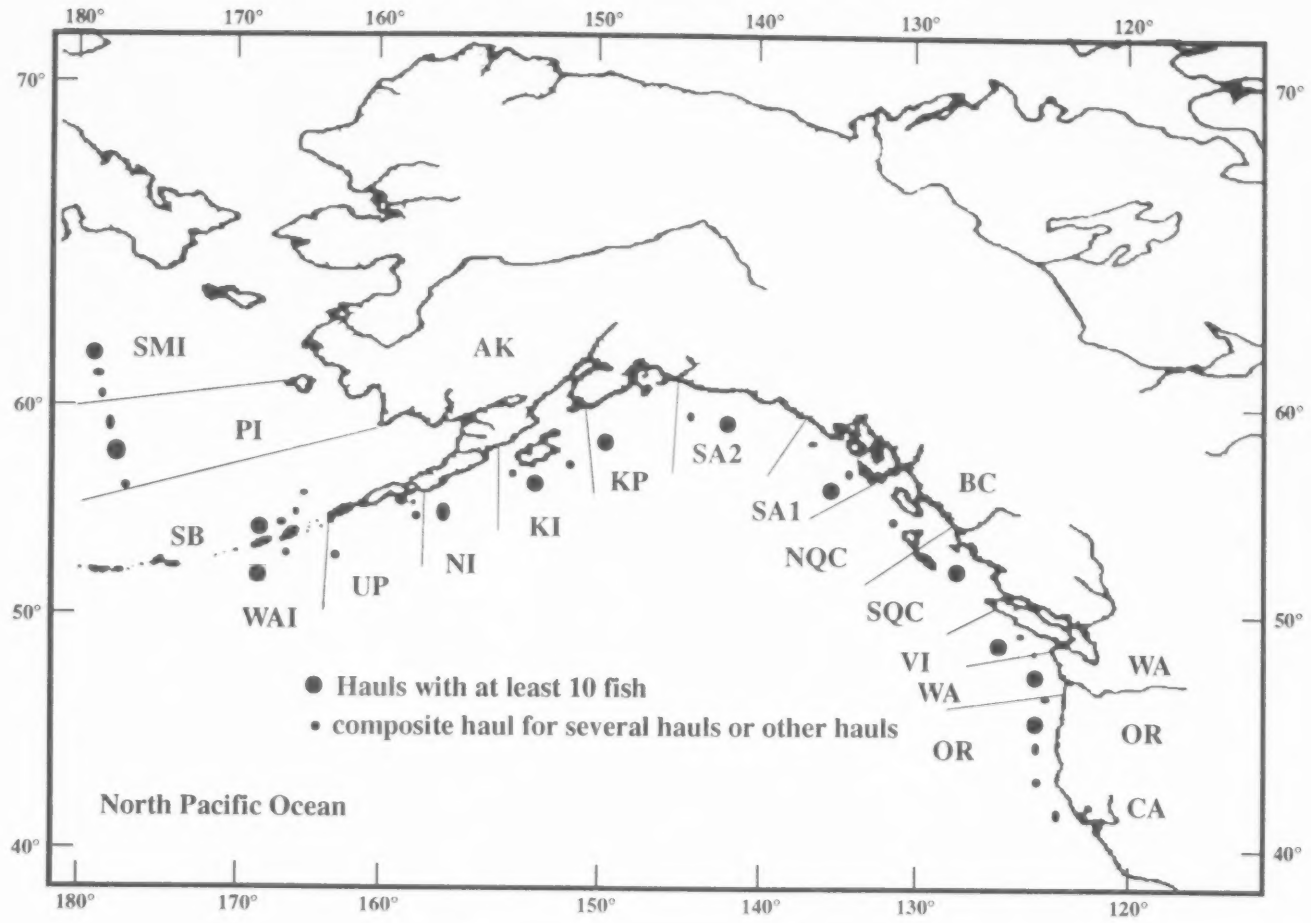

Figure 3.1. Sampling sites for 336 adult Pacific halibut, *Hippoglossus stenolepis*, in the northeast Pacific. Abbreviations are as in Table 3.1.

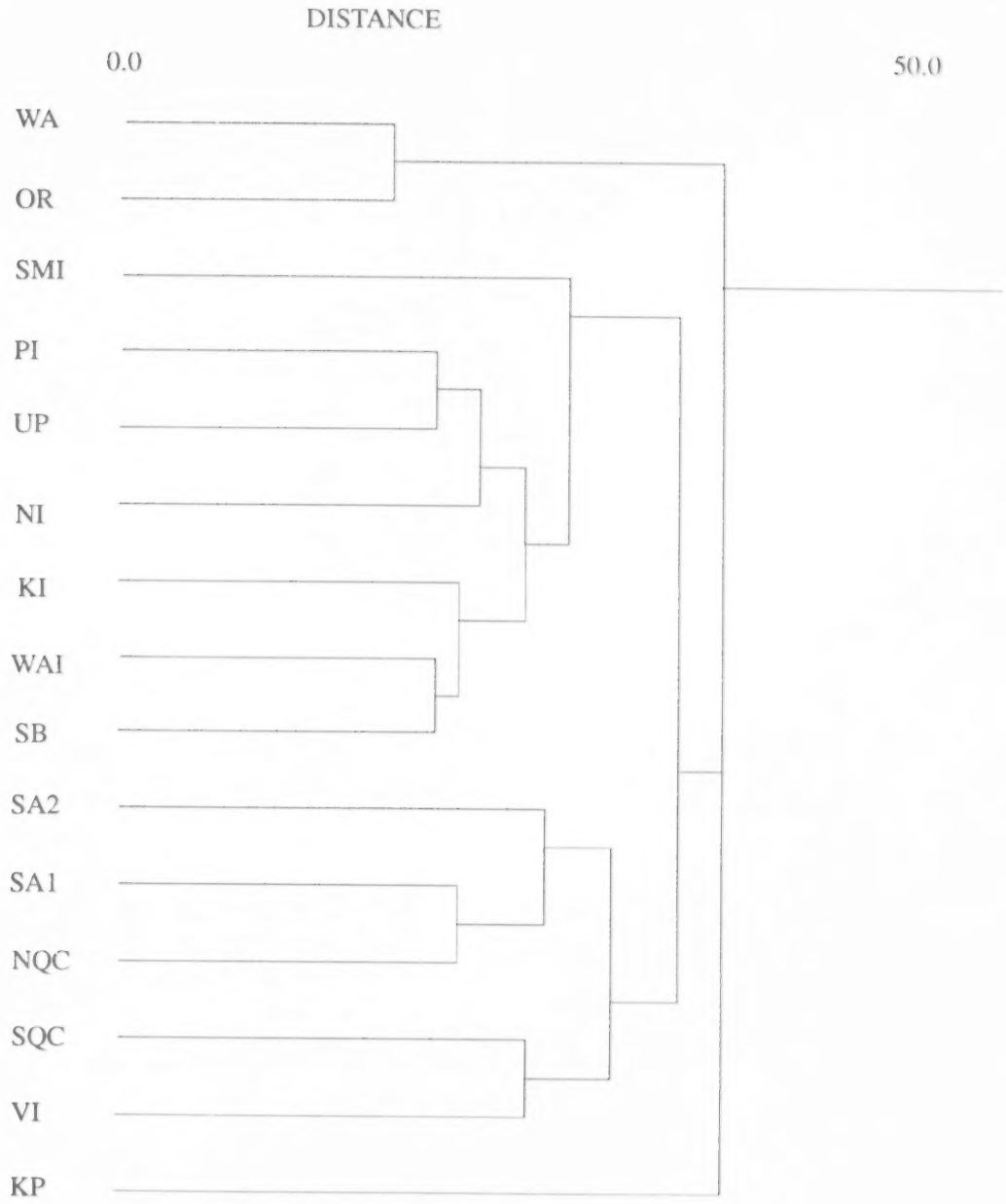

Figure 3.2. Cluster of parasites of Pacific halibut, *Hippoglossus stenolepis*, from 15 sampling localities based on prevalences using Euclidean Distance and average linkage. Abbreviations are as in Table 3.1. Geographic locations shown in Figure 3.1.

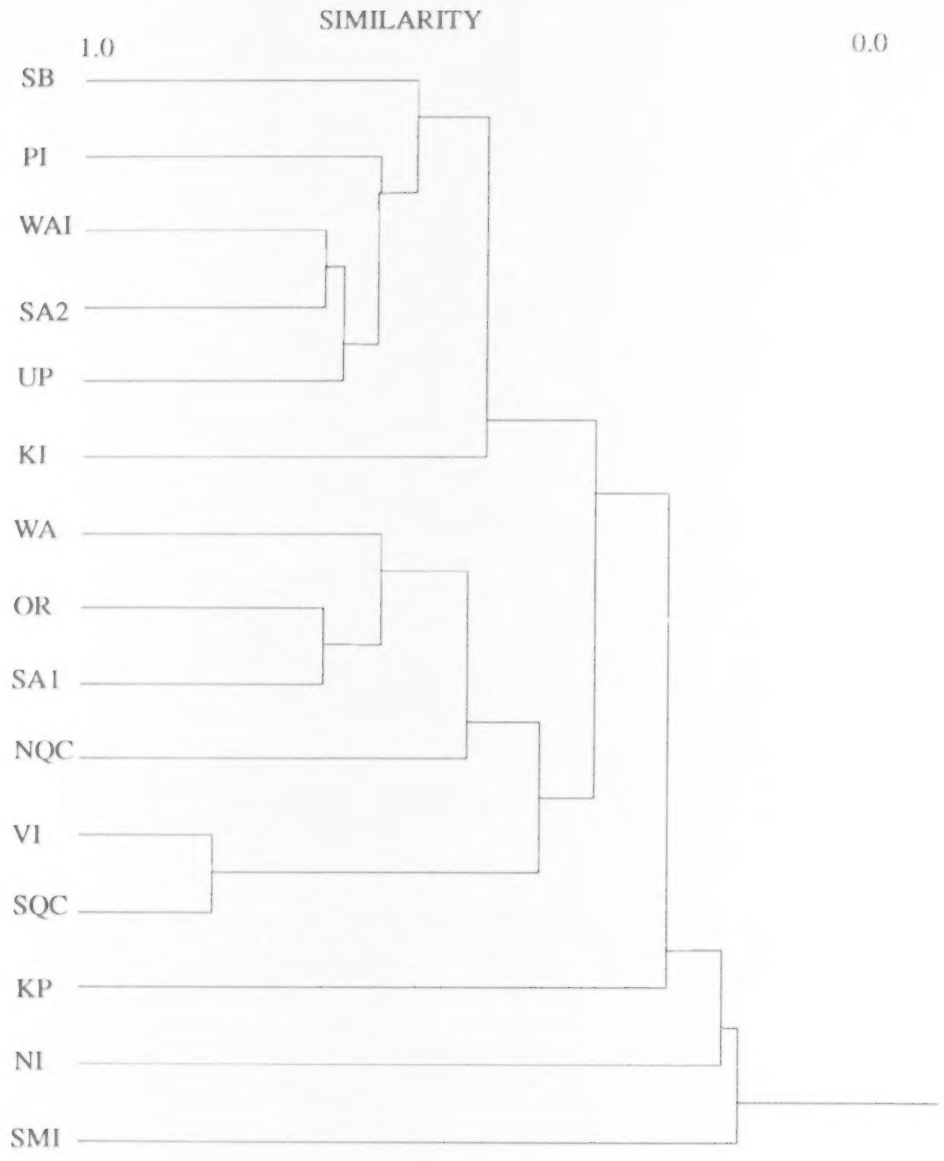

Figure 3.3. Cluster of parasites of Pacific halibut, Hippoglossus stenolepis, from 15 sampling localities using percentage similarity and average linkage. Abbreviations are as in Table 3.1. Geographic locations shown in Figure 3.1.

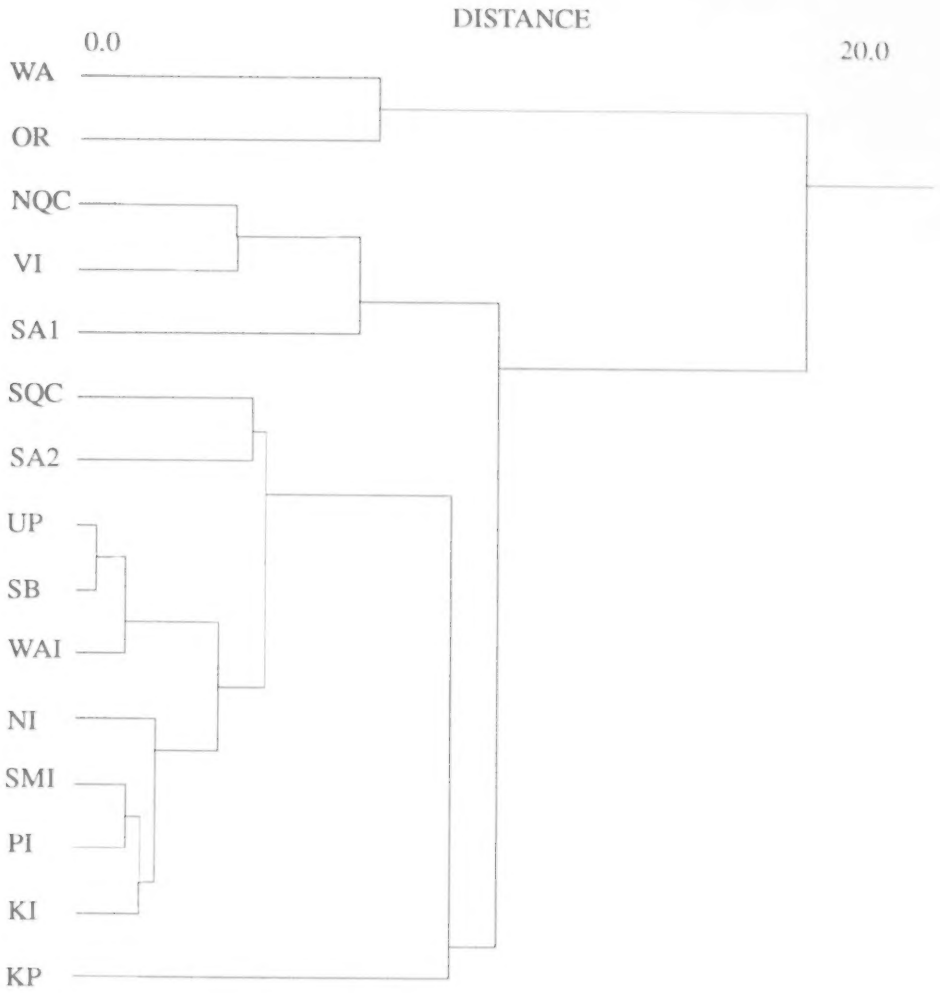

Figure 3.4. Cluster of parasites of Pacific halibut, Hippoglossus stenolepis, from 15 sampling localities based on parasite numbers using Euclidean Distance and average linkage. Widespread common and rare species (coded A and C in Appendix 3.1) excluded. Abbreviations are as in Table 3.1. Geographic localities shown in Figure 3.1.

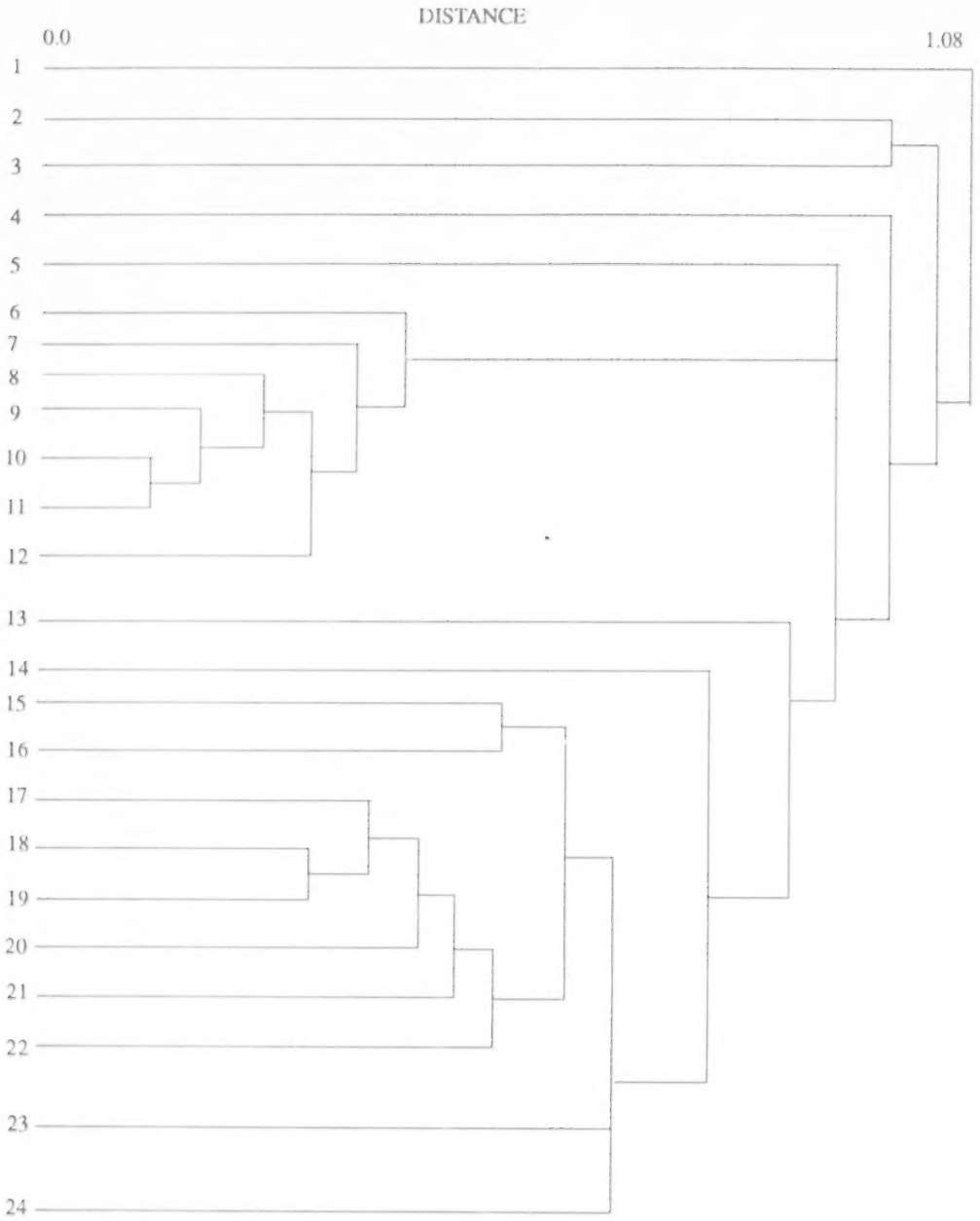

Figure 3.5. Cluster of parasites of 336 individual Pacific halibut, *Hippoglossus stenolepis*, using Euclidean Distance and average linkage. Cluster numbers correspond to those in Table 3.4. Cluster membership shown in Table 3.4.

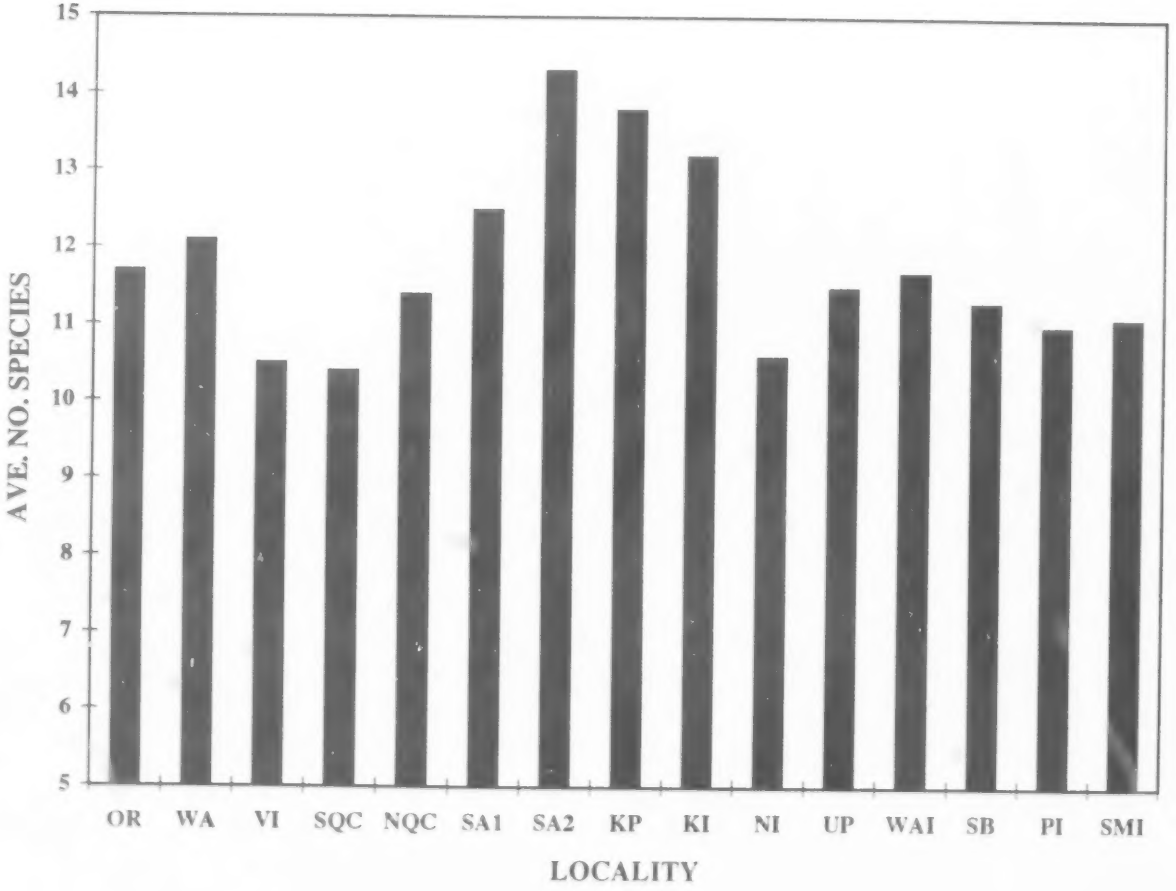

Figure 3.6. Average number of parasite species in Pacific halibut, *Hippoglossus stenolepis*, in the 15 localities. Sample sizes can be calculated from Table 3.1.

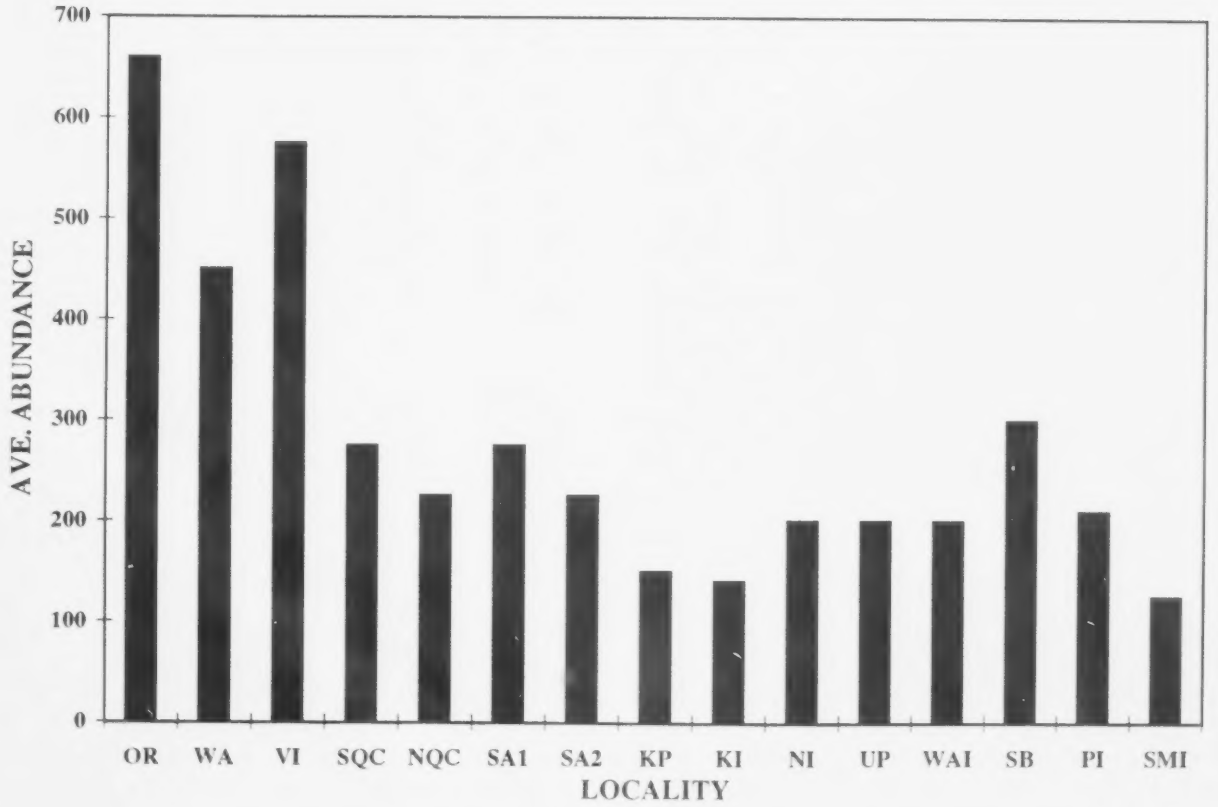

Figure 3.7. Average parasite abundance in Pacific halibut, *Hippoglossus stenolepis*, in the 15 localities. Sample sizes can be calculated from Table 3.1.

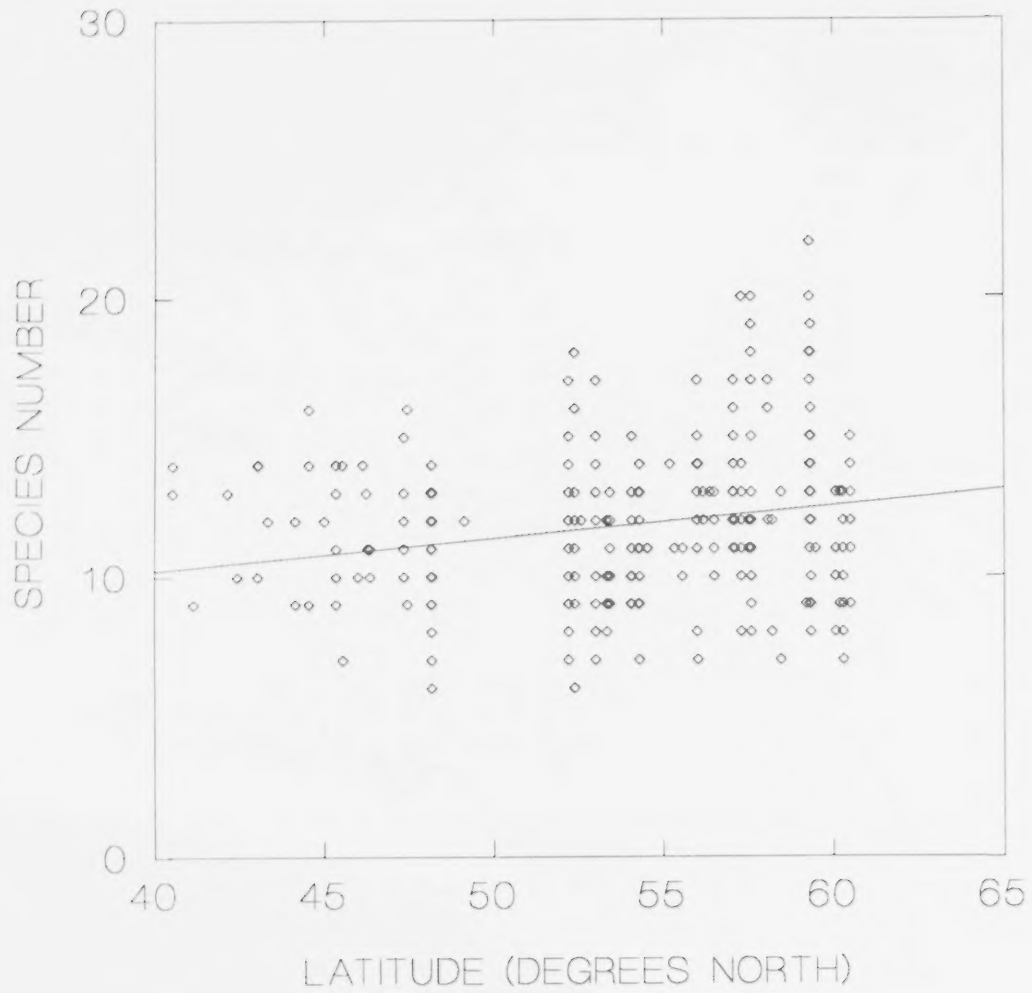

Figure 3.8. Numbers of parasite species in individual Pacific halibut, *Hippoglossus stenolepis*, as a function of latitude (°N).

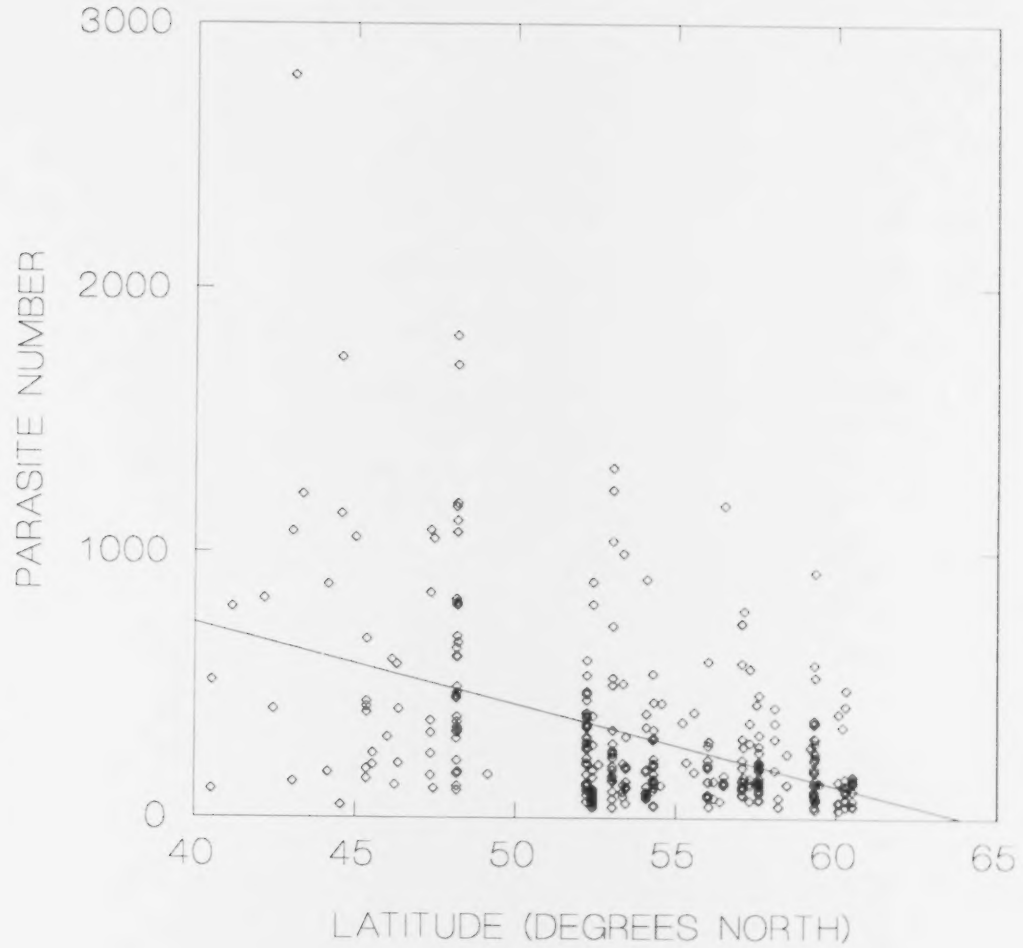

Figure 3.9. Numbers of parasite individuals in individual Pacific halibut, *Hippoglossus stenolepis*, as a function of latitude (°N).

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Appendix 3.1. Summary of prevalences and intensities ± SD for each parasite species from Pacific halibut, *Hippoglossus stenolepis*, by locality. Species names are abbreviated as the first three letters of each of the generic and specific epithet. The order of species is as in Table 2.1. Abbreviations for localities are as in Table 3.1. A = species present everywhere at similar levels of infection, B = species spotty in distribution, C = species rare and discontinuous, D = species found in contiguous localities.

			CERDRE	CERPLA	KUDTHY	LEPTOU	LEPTOG	MYXINC	UNIMUS	ZSCHSP	ENTHIP	ENTPUG	APOSIM	BRACRE	BUCEPH	DERVAR
	CODE		B	D	B	A	D	B	B	C	A	A	A	D	D	A
	N															
OR	23	PREV	4.3	21.7	13.0	21.7	4.3	4.3	0.0	0.0	47.8	65.2	34.8	0.0	0.0	47.8
		INT									5.9	6.4	1.5	0.0	0.0	17.4
		SD									4.5	4.3	0.8	0.0	0.0	57.5
WA	14		0.0	14.3	0.0	0.0	14.3	0.0	7.1	0.0	50.0	100.0	28.6	0.0	0.0	78.6
											5.1	17.1	2.0	0.0	0.0	5.5
											4.5	4.3	0.8	0.0	0.0	57.5
VI	32		0.0	21.9	6.3	3.1	6.3	6.3	0.0	0.0	93.8	71.9	15.6	0.0	0.0	21.9
											8.3	18.2	1.8	0.0	0.0	5.4
											15.6	26.0	0.4	0.0	0.0	4.5
SQC	31		0.0	22.6	0.0	38.7	6.5	3.2	0.0	3.2	93.5	96.8	6.5	16.1	0.0	35.5
											3.7	6.4	1.0	1.2	0.0	2.1
											2.6	6.1	0.0	0.4	0.0	2.2
NQC	8		0.0	12.5	0.0	37.5	0.0	25.0	12.5	0.0	100.0	87.5	12.5	12.5	0.0	0.0
											12.1	6.7	1.0	2.0	0.0	0.0
											11.2	8.2	0.0	0.0	0.0	0.0
SA1	20		5.0	40.0	5.0	25.0	5.0	25.0	5.0	0.0	95.0	90.0	20.0	50.0	5.0	25.0
											9.2	7.1	1.5	6.7	3.0	6.0
											9.8	8.5	1.0	11.7	0.0	6.4
SA2	30		10.0	40.0	10.0	30.0	0.0	20.0	20.0	0.0	96.7	93.3	23.3	66.7	6.7	30.0
											7.9	5.9	1.1	18.4	1.0	3.8
											7.7	6.5	0.4	19.1	0.0	2.3
KP	21		0.0	14.3	4.8	23.8	0.0	9.5	0.0	0.0	100.0	76.2	19.0	9.5	0.0	23.8
											12.4	9.7	1.3	1.5	0.0	1.8
											6.0	6.4	0.5	0.7	0.0	1.1
KI	26		3.8	57.7	3.8	30.8	0.0	11.5	26.9	0.0	84.6	100.0	15.4	7.7	0.0	57.7
											8.7	10.4	1.0	1.0	0.0	7.3
											5.8	8.4	0.0	0.0	0.0	10.6
NI	14		7.1	85.7	0.0	14.3	0.0	0.0	21.4	0.0	85.7	100.0	0.0	7.1	0.0	92.9
											3.2	9.6	0.0	1.0	0.0	32.9
											2.2	10.4	0.0	0.0	0.0	46.3
UP	20		0.0	85.0	5.0	30.0	0.0	0.0	30.0	0.0	95.0	95.0	45.0	5.0	5.0	60.0
											6.5	9.6	1.1	1.0	2.0	7.6
											4.4	6.8	0.3	0.0	0.0	11.9
WAI	21		5.0	50.0	0.0	20.0	0.0	0.0	5.0	0.0	90.0	95.0	10.0	0.0	15.0	40.0
											3.8	6.6	1.0	0.0	2.7	6.2
											4.0	5.2	0.0	0.0	2.9	9.5
SB	31		0.0	58.1	0.0	32.3	0.0	29.0	29.0	0.0	100.0	77.4	12.9	25.8	3.2	35.5
											10.4	4.3	2.0	1.6	1.0	2.4
											9.3	6.5	1.2	1.4	0.0	1.8
PI	14		0.0	78.6	0.0	7.1	0.0	7.1	21.4	0.0	78.6	85.7	35.7	0.0	35.7	85.7
											6.9	7.0	1.0	0.0	4.2	14.9
											4.1	4.1	0.0	0.0	4.5	37.0
SMI	31		12.9	38.7	0.0	16.1	0.0	6.5	19.4	0.0	67.7	83.9	22.6	25.8	12.9	80.6
											3.7	6.0	2.4	1.1	1.3	7.7
											2.8	5.3	2.1	0.4	0.5	9.7

	DISLAE	GENLAT	GONPHY	HEMLEV	LAMPSP	LECGIB	LECPHY	LEPOCSP	OTODSP	PARMER	PODGIB	PODOSP	PROBAS	PRCHSP	PSENOS	STEFOR
	D	D	D	B	C	D	C	C	D	D	D	D	D	C	C	A
OR	0.0	0.0	0.0	0.0	0.0	4.3	0.0	0.0	43.5	0.0	0.0	0.0	65.2	0.0	0.0	30.4
	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	14.3	0.0	0.0	0.0	12.1	0.0	0.0	3.7
	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.8	0.0	0.0	0.0	14.0	0.0	0.0	6.0
WA	0.0	0.0	0.0	0.0	7.1	0.0	0.0	7.1	35.7	0.0	0.0	0.0	71.4	7.1	0.0	35.7
	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0	32.0	0.0	0.0	0.0	24.0	2.0	0.0	2.0
	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.8	0.0	0.0	0.0	14.0	0.0	0.0	6.0
VI	0.0	0.0	0.0	0.0	0.0	18.8	0.0	0.0	9.4	0.0	3.1	0.0	81.3	0.0	0.0	21.9
	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	18.3	0.0	12.0	0.0	5.6	0.0	0.0	1.0
	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	30.0	0.0	0.0	0.0	5.9	0.0	0.0	0.0
SQC	0.0	0.0	0.0	9.7	0.0	38.7	0.0	0.0	38.7	0.0	3.2	0.0	3.2	12.9	0.0	22.6
	0.0	0.0	0.0	3.7	0.0	28.4	0.0	0.0	8.3	0.0	1.0	0.0	1.0	4.8	0.0	1.3
	0.0	0.0	0.0	3.8	0.0	32.1	0.0	0.0	13.9	0.0	0.0	0.0	0.0	5.6	0.0	0.8
NQC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	37.5	0.0	0.0	0.0	12.5	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.7	0.0	0.0	0.0	2.0	0.0	0.0	0.0
	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SA1	0.0	0.0	0.0	5.0	0.0	10.0	0.0	0.0	35.0	5.0	0.0	5.0	25.0	0.0	0.0	10.0
	0.0	0.0	0.0	2.0	0.0	1.5	0.0	0.0	13.0	1.0	0.0	6.0	4.2	0.0	0.0	1.0
	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	11.0	0.0	0.0	0.0	4.1	0.0	0.0	0.0
SA2	10.0	0.0	6.7	3.3	0.0	23.3	3.3	3.3	23.3	0.0	20.0	3.3	53.3	0.0	0.0	23.3
	1.0	0.0	1.0	1.0	0.0	1.9	1.0	1.0	7.4	0.0	2.8	1.0	6.8	0.0	0.0	1.6
	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	10.3	0.0	2.4	0.0	6.4	0.0	0.0	0.8
KP	0.0	0.0	0.0	28.6	0.0	38.1	0.0	0.0	14.3	0.0	76.2	0.0	4.8	0.0	0.0	9.5
	0.0	0.0	0.0	1.2	0.0	3.0	0.0	0.0	2.0	0.0	45.1	0.0	1.0	0.0	0.0	1.0
	0.0	0.0	0.0	0.4	0.0	2.6	0.0	0.0	1.7	0.0	54.2	0.0	0.0	0.0	0.0	0.0
KI	11.5	0.0	3.8	11.5	0.0	7.7	0.0	3.8	3.8	0.0	7.7	7.7	0.0	0.0	0.0	26.9
	14.7	0.0	1.0	1.0	0.0	4.5	0.0	1.0	1.0	0.0	5.5	1.0	0.0	0.0	0.0	1.7
	10.3	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0	2.1	0.0	0.0	0.0	0.0	1.3
NI	0.0	14.3	0.0	0.0	0.0	7.1	0.0	0.0	7.1	0.0	0.0	0.0	0.0	0.0	0.0	7.1
	0.0	1.5	0.0	0.0	0.0	9.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0
	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
UP	5.0	5.0	0.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	5.0	5.0	5.0	0.0	0.0	20.0
	2.0	2.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	9.0	3.0	1.0	0.0	0.0	1.3
	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
WAI	0.0	5.0	5.0	0.0	0.0	10.0	0.0	0.0	5.0	0.0	0.0	5.0	5.0	5.0	5.0	65.0
	0.0	1.0	1.0	0.0	0.0	1.5	0.0	0.0	1.0	0.0	0.0	2.0	1.0	1.0	2.0	6.2
	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.5
SB	6.5	0.0	22.6	0.0	0.0	6.5	0.0	0.0	0.0	3.2	0.0	0.0	3.2	0.0	0.0	25.8
	1.5	0.0	1.9	0.0	0.0	2.0	0.0	0.0	0.0	1.0	0.0	0.0	2.0	0.0	0.0	5.3
	0.7	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.6
PI	7.1	0.0	14.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.4	0.0	0.0	14.3
	5.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	1.0
	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SMI	9.7	0.0	3.2	38.7	0.0	6.5	0.0	0.0	3.2	3.2	0.0	3.2	6.5	9.7	0.0	41.9
	2.7	0.0	1.0	1.8	0.0	2.0	0.0	0.0	1.0	2.0	0.0	1.0	1.0	1.0	0.0	10.0
	2.9	0.0	0.0	1.1	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	30.1

	STEVET	TUBLIN	DIGESP	ZOODEX	BOTSCO	NYBSUR	SCOPLI	SCOPLG	TRYPAN	TETRAP	ANISIM	ASCFIL	CAPMAR	CONTSP	CUCHET	HYSADU
	C	A	C	C	C	D	D	D	C	C	A	C	D	D	D	A
OR	0.0	73.9	4.3	4.3	0.0	17.4	60.9	39.1	0.0	0.0	100.0	0.0	4.3	0.0	17.4	73.9
	0.0	374.4	1.0	1.0	0.0	2.8	34.1	8.8	0.0	0.0	258.2	0.0	1.0	0.0	1.5	3.6
	0.0	471.2	0.0	0.0	0.0	2.9	72.5	14.1	0.0	0.0	520.2	0.0	0.0	0.0	1.0	3.6
WA	0.0	78.6	0.0	0.0	0.0	14.3	57.1	35.7	7.1	0.0	100.0	0.0	0.0	0.0	21.4	50.0
	0.0	179.9	0.0	0.0	0.0	4.0	7.3	5.2	282.0	0.0	122.2	0.0	0.0	0.0	3.3	3.1
	0.0	471.2	0.0	0.0	0.0	2.9	72.5	14.1	0.0	0.0	520.2	0.0	0.0	0.0	1.0	3.6
VI	0.0	96.9	0.0	0.0	0.0	18.8	90.6	37.5	0.0	3.1	100.0	0.0	3.1	3.1	3.1	31.3
	0.0	124.2	0.0	0.0	0.0	16.0	40.4	3.8	0.0	3.0	381.4	0.0	10.0	1.0	1.0	4.8
	0.0	178.6	0.0	0.0	0.0	31.9	391.1	3.0	0.0	0.0	357.1	0.0	0.0	0.0		4.5
SQC	3.2	90.3	0.0	0.0	0.0	3.2	71.0	0.0	0.0	0.0	100.0	0.0	6.5	0.0	0.0	12.9
	1.0	61.3	0.0	0.0	0.0	1.0	17.8	0.0	0.0	0.0	167.8	0.0	14.5	0.0	1.0	1.0
	0.0	84.7	0.0	0.0	0.0	0.0	18.7	0.0	0.0	0.0	101.4	0.0	16.3	0.0	0.0	0.0
NQC	0.0	87.5	0.0	0.0	0.0	50.0	87.5	25.0	0.0	0.0	100.0	0.0	0.0	50.0	0.0	12.5
	0.0	72.0	0.0	0.0	0.0	13.3	60.0	2.0	0.0	0.0	76.1	0.0	0.0	3.8	0.0	1.0
	0.0	117.9	0.0	0.0	0.0	23.8	53.9	1.4	0.0	0.0	47.6	0.0	0.0	4.9	0.0	0.0
SA1	0.0	95.0	0.0	0.0	0.0	30.0	55.0	40.0	0.0	0.0	100.0	0.0	0.0	40.0	0.0	10.0
	0.0	120.3	0.0	0.0	0.0	11.8	59.8	3.5	0.0	0.0	81.8	0.0	0.0	3.5	0.0	1.0
	0.0	243.0	0.0	0.0	0.0	25.1	111.4	1.2	0.0	0.0	141.1	0.0	0.0	2.2	0.0	0.0
SA2	0.0	93.3	0.0	0.0	0.0	53.3	36.7	46.7	0.0	0.0	100.0	0.0	10.0	43.3	3.3	10.0
	0.0	112.6	0.0	0.0	0.0	3.9	18.4	6.6	0.0	0.0	42.7	0.0	2.0	2.8	43.0	2.0
	0.0	197.2	0.0	0.0	0.0	3.7	21.2	7.3	0.0	0.0	56.1	0.0	1.0	2.0	0.0	1.7
KP	0.0	81.0	0.0	0.0	0.0	42.9	71.4	66.7	0.0	0.0	100.0	0.0	28.6	61.9	0.0	47.6
	0.0	38.9	0.0	0.0	0.0	4.2	3.8	12.9	0.0	0.0	33.6	0.0	63.2	3.0	0.0	4.4
	0.0	40.7	0.0	0.0	0.0	3.9	3.3	9.0	0.0	0.0	22.1	0.0	63.0	3.1	0.0	3.4
KI	0.0	88.5	0.0	0.0	0.0	65.4	61.5	46.2	0.0	0.0	100.0	0.0	19.2	50.0	3.8	38.5
	0.0	51.7	0.0	0.0	0.0	29.5	5.1	8.3	0.0	0.0	30.6	0.0	17.4	3.5	1.0	3.1
	0.0	49.5	0.0	0.0	0.0	106.6	6.7	8.8	0.0	0.0	27.3	0.0	23.8	3.2	0.0	2.9
NI	0.0	50.0	0.0	0.0	0.0	42.9	7.1	7.1	0.0	7.1	100.0	0.0	0.0	0.0	7.1	28.6
	0.0	22.7	0.0	0.0	0.0	36.7	3.0	3.0	0.0	39.0	88.4	0.0	0.0	0.0	4.0	1.8
	0.0	24.2	0.0	0.0	0.0	81.5	0.0	0.0	0.0	0.0	66.6	0.0	0.0	0.0	0.0	1.0
UP	0.0	70.0	0.0	0.0	0.0	55.0	20.0	5.0	0.0	0.0	100.0	0.0	5.0	15.0	5.0	20.0
	0.0	113.4	0.0	0.0	0.0	2.7	3.3	2.0	0.0	0.0	53.3	0.0	1.0	2.0	1.0	3.5
	0.0	226.9	0.0	0.0	0.0	2.1	2.1	0.0	0.0	0.0	43.8	0.0	0.0	1.0	0.0	3.3
WAI	0.0	70.0	5.0	0.0	10.0	40.0	25.0	25.0	0.0	0.0	95.0	0.0	10.0	35.0	5.0	55.0
	0.0	156.6	1.0	0.0	1.5	14.3	4.6	2.0	0.0	0.0	41.5	0.0	6.0	1.4	2.0	5.0
	0.0	281.9	0.0	0.0	0.7	35.5	5.5	1.7	0.0	0.0	54.3	0.0	7.1	0.5	0.0	6.3
SB	0.0	77.4	0.0	0.0	0.0	51.6	38.7	6.5	0.0	0.0	100.0	0.0	6.5	41.9	0.0	51.6
	0.0	335.4	0.0	0.0	0.0	6.4	2.8	1.5	0.0	0.0	38.2	0.0	1.0	2.7	0.0	6.9
	0.0	369.4	0.0	0.0	0.0	12.6	2.1	0.0	0.0	0.0	33.8	0.0	0.0	4.1	0.0	6.7
PI	0.0	71.4	0.0	0.0	0.0	57.1	21.4	0.0	0.0	0.0	100.0	0.0	0.0	14.3	0.0	21.4
	0.0	169.4	0.0	0.0	0.0	34.6	1.3	0.0	0.0	0.0	21.5	0.0	0.0	1.0	0.0	1.0
	0.0	253.6	0.0	0.0	0.0	69.2	0.6	0.0	0.0	0.0	22.3	0.0	0.0	0.0	0.0	0.0
SMI	0.0	58.1	0.0	0.0	0.0	61.3	12.9	0.0	0.0	3.2	87.1	0.0	0.0	9.7	3.2	12.9
	0.0	50.2	0.0	0.0	0.0	26.4	3.0	0.0	0.0	2.0	10.6	0.0	0.0	3.0	1.0	1.5
	0.0	105.5	0.0	0.0	0.0	69.8	2.8	0.0	0.0	0.0	10.0	0.0	0.0	3.5	0.0	0.6

	PARPAR	PSEDEC	SPIRGSP	BOLBSP	CORENH	CORSTR	CORVIL	ECHGAD	ACAHIP	GNALAR	LEPBIF	LEPHOS	LEPPAR	LEPPRA	OPITRI	HIRUDI
	D	A	D	D	D	A	D	A	A	D	C	C	A	C	D	D
OR	78.3	43.5	21.7	0.0	0.0	52.2	73.9	17.4	65.2	0.0	4.3	0.0	4.3	0.0	4.3	0.0
	81.1	2.5	1.4	0.0	0.0	5.6	7.9	3.3	3.7	0.0	1.0	0.0	1.0	0.0	1.0	0.0
	177.4	2.1	0.5	0.0	0.0	6.4	5.4	4.5	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WA	85.7	21.4	50.0	0.0	0.0	50.0	71.4	28.6	85.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	102.1	2.3	11.0	0.0	0.0	6.3	6.3	6.8	4.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	177.4	2.1	0.5	0.0	0.0	6.4	5.4	4.5	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
VI	15.6	15.6	3.1	0.0	0.0	43.8	93.8	28.1	78.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	7.6	1.2	1.0	0.0	0.0	3.6	8.8	2.3	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	9.8	0.4	0.0	0.0	0.0	5.2	7.4	1.7	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SQC	9.7	12.9	0.0	0.0	0.0	38.7	93.5	45.2	93.5	0.0	0.0	0.0	6.5	0.0	0.0	0.0
	14.3	1.5	0.0	0.0	0.0	1.8	13.7	7.1	2.8	0.0	0.0	0.0	1.0	0.0	0.0	0.0
	23.1	0.6	0.0	0.0	0.0	1.5	24.3	12.6	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
NQC	25.0	25.0	0.0	0.0	0.0	25.0	100.0	0.0	100.0	0.0	0.0	0.0	25.0	0.0	50.0	0.0
	7.5	2.0	0.0	0.0	0.0	2.0	5.9	0.0	3.0	0.0	0.0	0.0	1.0	0.0	4.0	0.0
	9.2	0.0	0.0	0.0	0.0	0.9	7.4	0.0	2.4	0.0	0.0	0.0	0.0	0.0	2.9	0.0
SA1	50.0	25.0	15.0	5.0	0.0	15.0	90.0	15.0	65.0	0.0	0.0	5.0	10.0	0.0	85.0	0.0
	54.6	3.2	2.3	1.0	0.0	1.7	10.9	2.0	2.6	0.0	0.0	1.0	1.0	0.0	6.6	0.0
	88.1	4.4	1.2	0.0	0.0	0.6	16.6	1.7	2.4	0.0	0.0	0.0	0.0	0.0	8.6	0.0
SA2	23.3	66.7	10.0	10.0	3.3	50.0	93.3	33.3	66.7	6.7	0.0	0.0	10.0	0.0	16.7	0.0
	30.1	3.1	2.0	1.0	1.0	1.9	15.7	6.5	2.5	1.0	0.0	0.0	1.0	0.0	1.4	0.0
	56.7	2.7	1.7	0.0	0.0	1.2	31.9	8.7	1.8	0.0	0.0	0.0	0.0	0.0	0.5	0.0
KP	9.5	28.6	9.5	14.3	4.8	19.0	95.2	71.4	38.1	33.3	0.0	0.0	38.1	0.0	61.9	0.0
	6.5	1.5	1.0	1.7	1.0	1.0	11.1	5.1	2.0	1.1	0.0	0.0	1.1	0.0	3.3	0.0
	2.1	1.2	0.0	0.6	0.0	0.0	12.4	5.9	1.6	0.4	0.0	0.0	0.4	0.0	2.5	0.0
KI	0.0	50.0	3.8	3.8	0.0	26.9	100.0	69.2	65.4	0.0	0.0	0.0	19.2	0.0	19.2	0.0
	0.0	1.9	1.0	2.0	0.0	1.3	13.5	11.2	3.2	0.0	0.0	0.0	1.2	0.0	2.4	0.0
	0.0	1.4	0.0	0.0	0.0	0.5	18.4	13.0	2.9	0.0	0.0	0.0	0.4	0.0	2.6	0.0
NI	0.0	64.3	0.0	0.0	0.0	7.1	85.7	57.1	71.4	7.1	0.0	0.0	21.4	0.0	35.7	0.0
	0.0	2.8	0.0	0.0	0.0	2.0	12.3	14.4	2.7	1.0	0.0	0.0	1.7	0.0	18.8	0.0
	0.0	2.0	0.0	0.0	0.0	0.0	14.4	21.7	2.2	0.0	0.0	0.0	0.6	0.0	30.3	0.0
UP	0.0	45.0	5.0	0.0	0.0	30.0	85.0	35.0	55.0	25.0	0.0	0.0	40.0	0.0	15.0	5.0
	0.0	1.4	1.0	0.0	0.0	2.0	29.6	5.0	4.5	4.2	0.0	0.0	1.0	0.0	2.3	1.0
	0.0	0.7	0.0	0.0	0.0	1.5	57.4	4.7	5.3	0.0	0.0	0.0	0.0	0.0	2.3	0.0
WAI	5.0	40.0	0.0	0.0	0.0	45.0	90.0	75.0	45.0	25.0	0.0	0.0	20.0	0.0	0.0	0.0
	1.0	2.3	0.0	0.0	0.0	2.0	13.8	6.5	2.3	3.4	0.0	0.0	1.0	0.0	0.0	0.0
	0.0	1.9	0.0	0.0	0.0	2.0	13.8	6.6	2.2	3.7	0.0	0.0	0.0	0.0	0.0	0.0
SB	12.9	35.5	3.2	0.0	0.0	35.5	90.3	54.8	16.1	0.0	0.0	0.0	16.1	0.0	6.5	3.2
	1.8	2.3	1.0	0.0	0.0	8.5	16.8	5.0	2.0	0.0	0.0	0.0	2.0	0.0	1.0	1.0
	1.0	1.6	0.0	0.0	0.0	18.2	23.4	6.3	1.7	0.0	0.0	0.0	2.2	0.0	0.0	0.0
PI	0.0	28.6	0.0	0.0	0.0	78.6	85.7	35.7	71.4	0.0	0.0	0.0	14.3	0.0	0.0	0.0
	0.0	2.3	0.0	0.0	0.0	9.0	34.4	2.2	3.1	0.0	0.0	0.0	1.0	0.0	0.0	0.0
	0.0	1.3	0.0	0.0	0.0	9.3	37.0	1.3	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SMI	0.0	22.6	0.0	0.0	0.0	87.1	100.0	45.2	16.1	0.0	0.0	0.0	12.9	0.0	9.7	19.4
	0.0	2.4	0.0	0.0	0.0	20.9	34.6	4.9	1.4	0.0	0.0	0.0	1.8	0.0	1.0	1.3
	0.0	1.8	0.0	0.0	0.0	25.3	55.2	7.5	0.5	0.0	0.0	0.0	0.5	0.0	0.0	0.8

CHAPTER 4 - STOCK DIFFERENTIATION

Halibut support one of the top five commercial fisheries in North America, with average annual landings of approximately 25,000 metric tons over the last 5 years (IPHC 1996), and are also widely sought in the sport fishery, thus contributing significantly to west coast economies. The International Pacific Halibut Commission (IPHC) is responsible for management of the resource. From the 1930's through the 1950's the IPHC recognized at least three stocks of halibut based on tagging experiments, egg and larval drift, anatomical differences, and differences in growth rate: those in the Bering Sea, those from the Gulf of Alaska south to Cape Spencer, Alaska (the vicinity of locality SA1) and those south of Cape Spencer (Skud 1977). These boundaries roughly followed the zoogeographic zonation in the North Pacific. Skud (1977) reanalyzed the data and concluded that there was extensive intermingling of fish among areas and no evidence to indicate that fish north and south of Cape Spencer, Alaska, constituted different stocks. Available biochemical evidence (Tsuyuki et al. 1969; Grant et al. 1984), though limited in scope and sampling effort, suggests little genetic variation throughout the northeast Pacific. As a result, the IPHC manages halibut as a single population, but with statistical divisions for management of data.

Parasites have been used successfully to distinguish populations or stocks of fishes and, as a result, provide information useful in fisheries management (see reviews by Lester 1990; Moser 1991, Williams et al. 1992). Gibson (1972) distinguished between three groups of *Platichthys flesus* from three different estuaries. With respect to the larger halibuts, Krzykawski and Wierzbicka (1982), using parasitological data and other information, distinguished between Barents Sea and Labrador stocks of Greenland halibut, *Reinhardtius hippoglossoides*. Khan et al. (1982) and Arthur and Albert (1993) used parasites to distinguish between Atlantic and Gulf of St. Lawrence stocks of *R. hippoglossoides*. No similar work on flatfishes has been done in the Pacific and, with the exception of Krzykawski and Wierzbicka (1982), there has been no attempt to distinguish between stocks of a species across a significant portion of the species' range.

In this chapter I use discriminant analysis of data on some of the parasites from Chapter 2 to determine if there are discrete populations or stocks of Pacific halibut in the northeast Pacific. I also do a

similar analysis on the juvenile fish and compare the results to the adult analysis to determine when any potential separation occurs.

MATERIALS AND METHODS

A total of 328 adults (202 of which were from 13 individual hauls (each with at least 10 fish)) ranging from northern California to the vicinity of St. Matthew's Island in the Bering Sea and 96 juveniles from five localities ranging from the northern Queen Charlotte Islands to the Bering Sea (see Chapter 3: Figure 3.1 and Table 3.1) were caught by staffs of the International Pacific Halibut Commission (IPHC) and the U.S. National Marine Fisheries Service during the summers of 1990-1992 (using longlines and trawls). Fish were bagged individually and immediately deep frozen at sea for later examination.

Fish and parasites were processed as outlined in Chapter 2.

Parasites used in the analyses were chosen based on the guidelines of Arthur and Albert (1993). Only those species with infections of long duration, no multiplication in the host, and relatively high abundance in at least one haul were used. Of the 59 parasite taxa identified in Chapter 2, 8 taxa met these criteria: the juvenile acanthocephalans *Corynosoma strumosum* and *C. villosum*, the metacestode *Nybelinia surmenicola*, the digenean metacercaria *Otodistomum* sp., and the larval nematodes *Anisakis simplex*, *Pseudoterranova decipiens*, *Contracaecum* sp., and Spirurid gen. sp.

Because individual fish varied extensively in size, and parasite numbers were strongly correlated with fish size (Chapter 2), parasite numbers were corrected for differences in host size. Parasite counts were first log transformed ($\ln(x+1)$). To adjust for the effect of fish length, a regression of the transformed parasite numbers on fish length for each species in each haul (plus the two extra localities)was calculated. This relationship was then used to adjust the parasite number within each fish in each haul (locality) to that expected for the average size fish in the overall sample (80.9 cm). These data were then used in discriminant function analysis. There are two valid ways of applying discriminant function analyses to data sets like these. I used the first, and most widely used, in which the data are divided into training and test sets, with a discriminant function calculated on the training set used to classify the test set. Interpretations are based on patterns in the test sets. The alternative is a bootstrapping method, in which a discriminant function, calculated after removal of an individual fish, is used to classify that fish; the process is repeated for each fish (for an example, see Arthur and Albert (1993)). Such a method makes use of the maximum amount of data in calculating the discriminant

function, and may increase the likelihood of correctly classifying similar fish. My method is more likely to suffer from sampling variation, particularly when prevalences are low, as they are in many of my subsamples. My choice of method was largely due to the fact that the statistical packages available to me do not use the bootstrapping method of cross validation.

My training set consisted of six fish randomly selected from each haul ("haul" training set) or these fish plus 4 from the northern Queen Charlotte Islands and 6 from Unimak Pass ("locality" training set). Discriminant functions calculated from data on these "training" fish were used to classify each of the remaining fish from each haul ("haul" test set) or those fish plus all remaining fish ("locality" test set). The test set fish were first classified into one of the 13 hauls or 15 localities. Classification matrices were examined for the degree of misclassification. Hauls or localities were then grouped and regrouped into 4 and 3 groups based on patterns in the 13 or 15 category analysis and the zoogeographic zones from Chapter 3. Analyses were then repeated. Classifications were examined for misclassification, and boundaries adjusted for retesting. Results presented are those from the best fit "test" classifications. Statistical analyses were performed in SYSTAT for Windows version 5.05 (Wilkinson et al. 1992).

RESULTS

Of the taxa that met the Arthur and Albert (1993) criteria, *N. surmenicola* was most common and abundant in northern localities and fairly common and abundant in central localities. *Corynosoma strumosum*, while variable in prevalence and abundance, was much more common in the northernmost localities. *C. villosum*, while prevalent everywhere, was more abundant in northern fish. *Otodistomum* sp. and Spirurid gen. sp. were more common and abundant in southern localities. *Anisakis simplex*, while present in virtually every fish from every locality, was more abundant in southern fish. *Pseudoterranova decipiens* and *Contracaecum* sp. appeared to be more common in central areas (Tables 4.1, 4.2). In the juveniles, *A. simplex* and *P. decipiens* were more common in central localities whereas *C. villosum*, *C. strumosum*, and *Hysterothylacium aduncum* were more common in northern localities (Table 4.3).

Thirteen (hauls) or 15 (localities) category discriminant analysis revealed severe misclassification in most areas. Only 31% of the fish were correctly classified to hauls (Table 4.4) and only 27.5% were correctly classified to locality (Table 4.5). The discriminant functions did assign correctly the majority of test fish from four hauls (12/14 Vancouver Island fish, 3/4 Southeast Alaska 1 fish, 3/5 from the Pribilof Islands, and all 4 from St. Matthew's Island) and two localities (19/26 from Vancouver Island and 14/22 from the southern Bering Sea). However, misclassification of fish from surrounding areas to these hauls indicated less than accurate separation. The clearest indications from these classifications are that localities from the vicinity of the Queen Charlotte Islands south should be grouped together, and there is a suggestion that the northern Bering Sea locations should be grouped.

Regrouping into 4 categories, using boundaries from my zoogeographic analyses (Chapter 3) plus the apparent northern Bering Sea grouping, considerably improved the predictive ability. The "best fit" four category grouping gave approximately 70% correct classification at the haul level (Table 4.6) and 62% at the locality level (Table 4.7). The boundaries of the northern groups differed slightly between haul and locality "best fit" analyses; however there was only a 1% difference in correct classification at the locality (haul) level using the boundaries from the haul (locality) analysis (not shown). Both haul and locality functions were good predictors for the Oregon to southern Queen Charlotte Islands fish; both classified over 80% of these southern

fish, and only 5% (haul) to 6% (locality) of the other fish were misclassified to this group. The haul function correctly classified all the St. Matthew's Island fish, and misclassified only 3% of the fish to this group; the locality analysis correctly classified over 70% of the Pribilof-St. Matthew Island fish, and only misclassified 7% of the other fish to this group. There is much misclassification in the other two groups. Adjusting this boundary did not produce marked improvement (not shown).

Grouping into 3 categories by combining the two central groups resulted in substantial improvement in classification (90% correct at the haul level and 83% correct at the locality level) (Tables 4.8 and 4.9). Shifting of the boundary between the northern and central group reveals that classification breaks down when the southern Bering Sea is included in the northern group (not shown). Inclusion of the northern Queen Charlotte Islands in the southern group has little effect (81% correct classification) (not shown). These analyses indicate a southern (Oregon - southern Queen Charlotte Islands) group, a central (northern Queen Charlotte Islands - southern Bering Sea)group, and a northern (PI-SMI) group.

Classification into 2 categories (with SQC as the dividing line) provided no improvement at the haul level (90.3% correct) and only a slight improvement at the locality level (87% correct) (not shown). Inclusion of NQC in the southern group had little effect (88% correct classification).

Classification of juveniles was poor with any organization of localities. The "best fit" classification correctly classified only 66% of the fish with substantial misclassification among the localities (Tables 4.10 and 4.11). Fish from the northern Queen Charlotte Islands through Nagai Island separated reasonably well, but the majority of fish from the northernmost locality were also misclassified to this group. However, the discriminating power of the function was probably low due to the low parasite numbers and prevalences in the juveniles (Table 4.3).

DISCUSSION

My finding that neither individual hauls nor localities provide good separation may be due, in part, to my use of the technique that divides the data into training and test sets rather than the bootstrapping technique. Also, I used a small set of larval parasites, all of which are known to be long-lived and do not multiply in the host. Other long-lived parasites such as the myxosporeans have been used in stock discrimination, but were not included here because of the lack of abundance data. However, the decreased ability to detect differences because of the small dataset is offset by the increased ability to detect the host's past activities. Most of these parasites live for at least several years; therefore, the presence and abundance of these parasites may record where the host has been over that time period. The abundance of all of these parasites increases with fish length, particularly since larger fish eat more fish and most of the parasites are transferred from other fish. Many of each of the species, however, are probably short-term acquisitions (last few years); thus, there is some bias to the more recent past.

Patterns of geographical variation in parasite distribution and abundance have provided fisheries managers with information useful for discrimination of stocks of fishes (see review by Lester 1990). The patterns are determined by the complex ecological interactions among nonuniform distributions of intermediate and definitive hosts and the environment. In my system, two major factors may govern these patterns. Temperature may be the primary factor. My system spans a wide geographic range that contains a wide variety of temperature regimes. In Chapter 3, I showed that the overall abundance of parasites decreases with latitude and suggested that temperature may govern this pattern. Thus, the increase in the abundance and prevalence of *Anisakis* and Spirurida gen. sp. in the south may be due to increased temperature in the south. Moreover, species such as *Nybelinia*, *Corynosoma strumosum*, *Pseudoterranova*, and *Contracaecum* may be distributed according to their temperature tolerances. *Nybelinia* and *Corynosoma strumosum* (northern species) may be cold adapted species. *Pseudoterranova* and *Contracaecum* (central species) may be adapted to intermediate temperatures. The other factor that may play a role in governing distributions may be the distributions of definitive or intermediate hosts. Margolis (1958) considered *Corynosoma villosum* a more northern species in accordance with the distribution of its primary definitive host, the Steller sea lion (*Eumetopias jubata*).

Although I find that *C. villosum* is prevalent everywhere, I do find it to be more abundant in northern localities. *Otodistomum* sp. is more common in southern localities in accordance with the distribution of its definitive hosts, the skate *Raja binoculata* and the spiny dogfish *Squalus acanthias* (Lloyd 1938; T. McDonald, DFO, Nanaimo, per. comm.; Hart 1973).

My results show three things: 1) no separation of juvenile fish, 2) a clear separation of southern adults and 3) a potential separation of the northernmost adults. Skud's (1977) analysis clearly indicates compensatory movement of juveniles from the Gulf of Alaska and southern Bering Sea to southern areas, and, as such, predicts that juveniles should have more similar parasite faunas among areas. My data show this similarity, which may support this movement; however, at least two factors prevent definitive conclusions. First, small fish are less likely than adults to harbor some parasites due to dietary differences and less time to develop a long-term fauna. The halibut involved are above the size where fish, the major transmitter of these long term parasites, become a significant portion of the diet (Best and St. Pierre 1986), but prevalences and intensities are low, hindering separation. Second, and maybe more important, most of my juvenile samples came from areas that form a single group in the classification of adults. The sample from the northern Queen Charlottes is near the southern boundary of that group, and the sample from Nunivak Island is near the northern boundary. Samples of juveniles from further south should be examined. Until further information is available, management should consider juveniles a mixed "stock", at least for the northern area. Such information warrants particular consideration in management because halibut at this stage are susceptible to bycatch (unintended catch) in other fisheries (IPHC 1996). Excessive bycatch of halibut at this stage may impact future halibut populations in distant localities.

My data suggest that there is some merit to the IPHC's early recognition of three "stocks" of adult halibut. Parasite data support the existence of two major "populations" of halibut, with a "subpopulation" in the central and northern Bering Sea. The high proportion of correct classifications based on parasites suggest that these differences are well established. Recognition of such stocks is also supported by several of Skud's (1977) observations. Skud (1977) suggested that juveniles home to the areas in which they were spawned. He then presented data suggesting that after fish home to spawning areas, southern and northern fish maintain

reasonably separate migration circuits between feeding and spawning grounds. Data from Skud (1977) and more recent tagging data (Geernaert 1996) also suggest that southern fish move less than their northern counterparts. Skud also recognized a resident population in the Bering Sea.

The patterns identified in this analysis both agree only in part with those in the zoogeographic analysis. The southern boundaries are both in the vicinity of the Queen Charlotte Islands, providing additional support to the existence of a "southern" stock of halibut. However, there is no sign of a division in the vicinity of Kodiak Island in this analysis, suggesting that the division near Kodiak Island depends on short-lived, temporary species. The evidence for the existence of a northern Bering Sea stock is equivocal; it was supported by the clustering of localities using prevalences and, to some degree, the clustering of individuals, but not by any other analyses.

Skud concluded that southern and northern groups mixed extensively at all ages of their life history and that, although populations of adults may be largely discrete in the summer, any such discreteness was temporary, because tagging evidence suggested more extensive winter migrations associated with spawning. Skud's conclusions pose two questions. First, do fish from different "stocks" mix extensively? Second, do such stocks represent reproductive units?

My analysis in this chapter is based on long-lived parasites, which presumably would reflect a relatively long history of movement. My data suggest less extensive movement in southern areas. Because parasites are generally more abundant in the south, southern fish may be more easily classified. Nevertheless, if the southern fish mingled extensively with more northern fish, there should be more similarity in the parasite faunas. In particular, central area fish should develop characteristics of southern fish. This does not happen as is shown by the very low proportion of central fish misclassified as southern fish (Table 4.9). My information cannot completely rule out the movement of southern fish to central areas during the spawning season, then back to southern areas for the feeding season. Their long-lived parasite fauna, having been established in the distinct southern areas, would probably not lose its southern character. Winter sampling could potentially address this issue.

With respect to the Bering Sea, I suggest that the majority of the mixing occurs in the southern Bering Sea since classification breaks down when the southern Bering Sea is included in the northern region. This is

consistent with larval studies that show that larvae enter the Bering Sea through the Aleutian chain. Those fish may not disperse far into the Bering Sea. Rather, they either remain in the southern Bering Sea or migrate back to the Gulf of Alaska area (Skud (1977) believed that both occurred). Migration may explain why fish tagged in the Bering Sea tend to be recovered at greater distances from the tagging site than those tagged elsewhere (Geernaert 1996). Migrations of the Bering Sea stock appear to be in a more northerly direction (Skud 1977), which would preclude their mixing in the Aleutians and the Gulf of Alaska. My zoogeographic analysis using patterns of prevalence (Chapter 3) showed that Bering Sea parasites are rarely found outside the Bering Sea.

The definitive answer to the question of whether these groups are reproductive stocks cannot be answered from this study. Molecular data may provide some clarification. Those studies done to date, however, have not because of limited sampling areas, the limited number of loci examined, and the use of juveniles only. Tsuyuki et al. (1969) examined a single serum hemoglobin transferrin locus in halibut from ten sites from Vancouver Island to the Bering Sea and found that only one southeast Alaska locality was different. Grant et al. (1984) found no differences between Gulf of Alaska and Bering Sea halibut at five loci. They also discounted Tsuyuki et al's. (1969) results as due to methodological error. Grant et al. (1984), however, were able to distinguish northeast Pacific halibut from Japanese halibut. However, Lester et al. (1988) pointed out that biochemical/genetic information measures differentiation at a different time scale than that reflected in parasite data. According to Grant (1984), movement of only a few Atlantic herring (*Clupea harengus*) may be sufficient to obscure true differences between different breeding stocks. Thus, even limited gene flow could obscure any differences in the loci examined over evolutionary time; parasite data may represent the histories of individual fish or groups of fish, a time scale of more importance to the management of stocks. Therefore, the parasite data presented in this study suggest that, to answer the question concerning reproductive stocks, molecular studies must address the issue of mixing in the Bering Sea, and most importantly, the possibility of a reproductive stock in the south. In the meantime, a conservative, though more complex, approach would dictate management of ecological stocks, thus possibly avoiding depletion of distant reproductive stocks by overexploitation of local mixtures of fish.

My analysis provides a much fuzzier picture than that of Arthur and Albert (1993) for Greenland halibut in the northwest Atlantic. Apart from the methodological differences, I'm not surprised. Arthur and

Albert were dealing with a very different system. Geological and oceanographic conditions around the Gulf of St. Lawrence are quite complex and create great potential for isolation of stocks. The northeast Pacific is much more open, with fewer isolating mechanisms. I have shown that the system is clinal (Chapter 3). Pacific halibut are quite capable of migrating along the entire Pacific coast; therefore, less clearcut divisions are expected. Nevertheless, I have successfully identified groups of fish, some with a high degree of accuracy.

I recognize that the complexity of the halibut's life history and the limited scope of my study in the context of the entire life history of halibut makes it difficult to establish stocks as completely independent. As Skud (1977) pointed out, we must consider all aspects of the life history in making management decisions. In the end, however, a knowledge of when, where, and how long stocks are discrete may make those decisions easier. Parasite data appear to have provided some useful information in this regard.

Table 4.1. Summary of parasites used for discrimination of stocks of adult Pacific halibut by haul.

	OR (n = 10)		WA (n = 10)		VI (n = 20)		SQC (n = 31)		SA1 (n = 10)		SA2 (n = 15)		KP (n = 21)	
Parasite	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity
Anisakis simplex	100	234.6±252.7	100	138±113.0	100	387.7±274.4	100	167.8±93.2	100	108±182.6	100	48.1±62.2	100	33.6±22.1
Corynosoma villosum	60	9.7±5.8	80	7.6±7.6	95	8.6±7.4	93.5	13.7±24.3	80	16±23.6	100	9.1±8.8	95.2	11.1±12.4
Corynosoma strumosum	30	1.7±0.6	50	7.6±5.5	45	3.7±6.2	38.7	1.8±1.5	0	0	60	1.7±0.9	19	1±0.0
Nybelinia surmenicola	10	2.0±0.0	10	1±0.0	20	3.0±2.8	3.2	1.0±0.0	10	2.0±0.0	53.3	3.6±2.3	42.9	4.2±3.9
Otodistomum sp.	30	7.3±3.5	30	7.3±8.5	5	1±0.0	38.7	8.3±13.9	20	17.0±12.7	26.7	5.0±6.7	14.3	2±1.7
Pseudoterranova decipiens	20	1.0±0.0	20	3.0±1.4	20	1.3±0.5	12.9	1.5±0.6	0	0	66.7	2.2±1.8	28.6	1.5±1.2
Contracaecum sp.	0	0	0	0	5	1±0.0	0	0	60	3.7±2.3	40	3.2±2.5	61.9	3.0±3.1
Spirurid gen . sp.	30	1.7±0.6	60	1.7±0.8	0	0	0	0	20	2.0±1.4	6.7	1±0	9.5	1±0

Table 4.1 (continued).

	KI (n = 12)		NI (n = 13)		WAI (n = 19)		SB (n = 20)		PI (n = 11)		SMI (n = 10)	
Parasite	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity
Anisakis simplex	100	35.9±34.8	100	80.3±62.0	100	35.6±48.8	100	45.2±34.5	100	24.8±24.2	100	11.6±10.9
Corynosoma villosum	100	19±23.3	84.6	12.6±15.0	94.7	14.3±14.0	95	20.1±27.2	81.8	27.1±37.0	100	19.3±17.8
Corynosoma strumosum	16.7	1.5±0.7	7.7	2.0±0.0	42.1	2.1±2.0	40	2.8±1.9	72.7	4.4±4.5	100	29.3±25.9
Nybelinia surmenicola	75	52.1±146.6	38.5	42.2±89.0	36.8	16.1±35.5	45	2.2±1.1	63.6	39.3±73.4	70	3.9±2.8
Otodistomum sp.	8.3	1±0.0	7.7	1±0.0	5.3	1±0.0	0	0	0	0	0	0
Pseudoterranova decipiens	33.3	2.8±2.4	61.3	2.5±2.0	42.1	2.5±2.0	40	2.4±1.6	27.3	2.3±1.5	30	2±1.73
Contracaecum sp.	41.7	2.4±0.0	0	0	31.6	1.3±0.5	35	1.4±0.5	18.2	1±0	10	1±0
Spirurid gen . sp.	8.3	1±0	0	0	0	0	5	1±0	0	0	0	0

OR = Oregon/northern California, WA = Washington, VI = southern Vancouver Island, SQ C= southern Queen Charlotte Islands, SA1= southeast Alaska 1, SA2 = southeast Alaska 2, KP = Kenai Peninsula, KI = Kodiak Island, NI = Nagai Island, WAI = western Aleutian Islands, SB = southern Bering Sea, PI = Pribilof Island (central Bering Sea), SMI = St. Matthew Island (northern Bering Sea)

Table 4.2. Summary of parasites used for discrimination of stocks of adult Pacific halibut by locality.

	OR (n = 23)		WA (n = 14)		VI (n = 32)		SQ C (n = 31)		NQC (n = 8)		SA 1(n = 20)		SA2 (n = 29)	
Parasite	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity
Anisakis simplex	100	258.2±520.2	100	122.2±101.0	100	381.4±357.1	100	167.8±101.4	100	76.1±47.6	100	81.8±141.1	100	44.0±57.0
Corynosoma villosum	73.9	7.9±5.4	71.4	6.3±7.3	93.8	8.8±7.4	93.5	13.7±24.3	100	5.9±7.4	90	10.9±16.6	93.1	16.1±32.0
Corynosoma strumosum	52.2	5.6±6.4	50	6.3±5.2	43.8	3.6±5.2	38.7	1.8±1.5	25	2.0±0.9	15	1.7±0.6	51.7	1.9±1.0
Nybelinia surmenicola	17.4	2.8±2.9	14.3	4.0±4.2	18.8	16.0±31.9	3.2	1.0±0.0	50	13.3±23.8	30	11.8±25.1	51.7	4.1±2.0
Otodistomum sp.	43.5	14.3±13.8	35.7	32±55.7	9.4	18.3±30.0	38.7	8.3±13.9	37.5	4.7±2.3	35	13.0±11.0	20.7	8.3±11.0
Pseudoterranova decipiens	43.5	2.5±2.1	21.4	2.3±1.5	15.6	1.2±0.4	12.9	1.5±0.6	25.0	2.0±0.0	25.0	3.2±4.4	69.0	3.1±3.0
Contracaecum sp.	0	0	0	0	3.1	1.0±0	0	0	50	3.8±4.9	40	3.5±2.2	44.8	2.0±2.0
Spirurid gen . sp.	21.7	1.4±0.5	50	11±24.7	3.1	1.0±0	0	0	0	0	15	2.3±1.2	10.3	2.8±2.0

Table 4.2 (continued).

	KP (n = 21)		KI (n = 26)		NI (n = 13)		UP (n = 20)		WAI (n = 20)		SB (n = 29)		PI (n = 14)	
Parasite	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity
Anisakis simplex	100	33.6±22.1	100	29.5±27.3	100	80.3±62.0	100	53.3±43.8	100	41.5±55.0	100	40.6±33.6	100	21.5±22.3
Corynosoma villosum	95.2	11.1±12.4	100	11.2±18.4	84.6	12.6±15.0	85	29.6±57.4	95	13.8±14.0	96.6	16.8±18.3	85.7	34.4±37.0
Corynosoma strumosum	19.0	1±0.0	26.9	1.3±0.5	7.7	2.0±0.0	30	2.0±1.5	40	2.1±2.0	37.9	8.5±20.2	78.6	9.0±9.3
Nybelinia surmenicola	42.9	4.2±3.9	65.4	29.5±106.6	38.5	42.2±89.0	55	2.7±2.1	35	16.1±33.8	51.7	6.7±13.1	57.1	34.6±69.2
Otodistomum sp.	14.3	2.0±1.7	3.8	1±0	7.7	1±0.0	0	0	5	1±0	0	0	0	0
Pseudoterranova decipiens	28.6	1.5±1.2	50	1.9±1.4	61.3	2.5±2.0	45	1.4±0.7	45	2.3±2.0	37.9	2.3±1.5	28.6	2.3±1.3
Contracaecum sp.	61.9	3.0±3.08	50	3.2±3.2	0	0	15	2.0±1.0	30	1.3±1.0	37.9	3.0±4.5	14.3	1.0±0
Spirurid gen . sp.	9.5	1.0±0	3.8	1±0.0	0	0	5	1.0±0.0	0	0	3.5	1±0.0	0	0

Table 4.2 (continued).

	SMI (n = 28)	
Parasite	%	Intensity
Anisakis simplex	83.9	10.9±10.0
Corynosoma villosum	90.3	34.4±55.9
Corynosoma strumosum	77.4	23.2±25.4
Nybelinia surmenicola	58.1	25.0±69.8
Otodistomum sp.	0	0
Pseudoterranova decipiens	22.6	2.4±1.8
Contracaecum sp.	6.5	4.0±3.5
Spirurid gen . sp.	0	0

OR = Oregon/northern California, WA = Washington, VI = southern Vancouver Island, SQ C= southern Queen Charlotte Islands, NQC = northern Queen Charlotte Islands, SA1= southeast Alaska 1, SA2 = southeast Alaska 2, KP = Kenai Peninsula, KI = Kodiak Island, NI = Nagai Island, WAI = western Aleutian Islands, SB = southern Bering Sea, PI, Pribilof Island (central Bering Sea), SMI = St. Matthew Island (northern Bering Sea)

Table 4.3. Summary of parasites used for discrimination of stocks of juvenile Pacific halibut.

	NQC (n = 20)		KI (n = 13)		NI (n = 20)		UP (n = 20)		PI (n = 23)	
Parasite	%	Intensity	%	Intensity	%	Intensity	%	Intensity	%	Intensity
Anisakis simplex	25.0	1.2	7.7	1.0±0	65.0	3.1±1.9	70.0	3.6±3.1	30.4	1.7±0.8
Corynosoma villosum	5.0	1±0.0	46.2	1.3±2.4	75.0	3.4±2.6	80	5.8±7.4	8.7	1.5±0.7
Corynosoma strumosum	0	0	7.7	1.0±0	0	0	5.0	1±0.0	47.8	1.2±0.4
Hysterothylacium aduncum	15.0	1±0.0	92.3	4.4±3.2	95.0	8.7±10.7	85.0	5.4±8.8	73.9	2.8±1.5
Nybelinia surmenicola	0	0	0	0	0	0	5.0	1±0.0	26.1	1.3±0.8
Pseudoterranova decipiens	0	0	7.7	1.0±0	25.0	1.4±0.9	15.0	1±0.0	4.4	6±0.0
Contracaecum sp.	0	0	15.4	1.0±0	10.0	5±5.7	0	0	0	0
Spirurid gen . sp.	0	0	0	0	5.0	2.0±0.0	0	0	0	0

NQC = northern Queen Charlotte Islands, NI = Nagai Island, UP = Unimak Pass, PI = Nunivak Island (central Bering Sea)

Table 4.4. Cross validation results of thirteen category discriminant function classification of adult Pacific halibut in the northeast Pacific using parasite data for individual hauls. Numbers of fish assigned to each haul and the corresponding percentage of the sample assigned to that category are shown. See Table 4.1 legend for key to abbreviations. Correct classifiations shown in bold (31.5% of 124).

	Assigned category												
True category	OR	WA	VI	SQC	SA1	SA2	KP	KI	NI	WAL	SB	PI	SMI
OR	**0**	2		1						1			
		50.0%		25.0%						25.0%			
WA	2	**0**											2
	50.0%												50.0%
VI			**12**	1						1			
			85.8%	7.1%						7.1%			
SQC	1	2	10	**11**						1			
	4.0%	8.0%	40.0%	**44.0%**						4.0%			
SA1					**3**							1	
					75.0%							25.0%	
SA2					1	**0**	1	1	1	1	3		1
					11.0%		11.0%	11.0%	11.0%	11.0%	33.0%		11.0%

Table 4.4 (continued)

True category	Assigned category												
	OR	WA	VI	SQC	SA1	SA2	KP	KI	NI	WAL	SB	PI	SMI
KP					7	1	**1**	1	1	3	1		
					46.7%	6.7%	**6.7%**	6.7%	6.7%	20.0%	6.7%		
KI					3			**1**		1		1	
					50.0%			**16.7%**		16.7%		16.7%	
NI			1	1				1	**2**	1		1	
			14.3%	14.3%				14.3%	**28.3%**	14.3%		14.3%	
WAL							3	1	1	**2**	5		
							23.1%	7.7%	7.7%	**15.3%**	38.5%		
SB		1 7.1%		1	3	2	1			1	**5**		
				7.1%	21.3%	14.2%	7.1%			7.1%	**35.5%**		
PI											1	**3**	1
											20.0%	**60.0%**	20.0%
SMI													**4**
													100%

Table 4.5. Cross validation results of 15 category discriminant function classification of adult Pacific halibut in the northeast Pacific using parasite data. for localities. Numbers of fish assigned to each locality and the corresponding percentage of the sample assigned to that category are shown. See Table 4.1 legend for key to abbreviations. Correct classifications shown in bold (39% of 250).

	Assigned category														
True category	OR	WA	VI	SQC	NQC	SA1	SA2	KP	KI	NI	UP	WAL	SB	PI	SMI
OR	**4**	2		1	2						2		3		
	17.3%	8.7%		4.3%	8.7%						8.7%		13.0%		
WA	2	**2**			1									1	2
	25.0%	**2.5%**			12.5%									12.5%	25.0%
VI		1	**19**	2	3							1			
		3.8%	**73.0%**	7.7%	11.5%							3.8%			
SQC	1	1	10	**11**							2				
	4.0%	4.0%	40.0%	**44.0%**							8.0%				
NQC					**2**	2									
					50.0%	50.0%									
SA1		1			1	**4**		1	1	1				3	
		7.1%			7.1%	**28.6%**		7.1%	7.1%	7.1%				21.4%	

Table 4.5 (continued)

True category	Assigned category														
	OR	WA	VI	SQC	NQC	SA1	SA2	KP	KI	NI	UP	WAL	SB	PI	SMI
SA2	1				1	2	**1**	3	3	1	1		8	1	1
	4.3%				4.3%	8.7%	**4.3%**	13.0%	13.0%	4.3%	4.3%		34.8%	4.3%	4.3%
KP						7	1	**1**	1	1	2		1		
						50.0%	7.1%	**7.1%**	7.1%	7.1%	14.3%		7.1%		
KI						7	2	1	**2**	1	2		3	2	
						35.0%	10.0%	5.0%	**10.0%**	5.0%	10.0%		15.0%	10.0%	
NI			1		1				2	**1**	1				
			14.3%		14.3%				28.6%	**14.3%**	14.3%				
UP			2			1			2	2	**1**	2	3		1
			14.3%			7.1%			14.3%	14.3%	**7.1%**	14.3%	21.4%		7.1%
WAI						3	1	1		2	2	**0**	5		
						21.4%	7.1%	7.1%		14.3%	14.3%		35.7%		
SB		1			1	4	3	1	2	1	2	5	**1**		2
		7.1%			7.1%	28.6%	21.4%	7.1%	14.3%	7.1%	14.3%	35.7%	**7.1%**		14.3%
PI													1	**3**	4
													12.5%	**37.5%**	50.0%

Table 4.5 (continued)

True category	Assigned category														
	OR	WA	VI	SQC	NQC	SA1	SA2	KP	KI	NI	UP	WAL	SB	PI	SMI
SMI						1			3			3		1 4.5%	**14**
						4.5%			13.6%			13.6%			**64.0%**

Table 4.6. Cross validation results of four category discriminant function classification of adult Pacific halibut (haul level) in the northeast Pacific using parasite data. Numbers of fish assigned to category and the corresponding percentage of the sample in that category are shown. Correct classifications shown in bold (70.2% of 124).

	Assigned category			
True category	OR-SQC	SA1-KP	KI-PI	SMI
OR-SQC	**41**	1	3	2
	87.2%	2.1%	6.4%	4.3%
SA1-KP		**15**	12	1 3.6%
		53.6%	42.9%	
KI-PI	4	13	**27**	1
	8.9%	28.9%	**60.0%**	2.2%
SMI				**4**
				100%

OR-SQC = Oregon/northern California to southern Queen Charlotte Islands, SA1-KP = southeast Alaska1 to Kenai Peninsula, KI-PI = Kodiak Island to Pribilof Islands, SMI = St. Matthew Island

Table 4.7. Cross validation results of four category discriminant function classification of adult Pacific halibut (locality level) in the northeast Pacific using parasite data. Numbers of fish assigned to category and the corresponding percentage of the sample in that category are shown. Correct classifications shown in bold (62% of 240).

	Assigned category			
True category	OR-SQC	NQC-KP	KI-SB	PI-SMI
OR-SQC	**60**	3	7	6
	78.9%	3.9%	9.2%	7.9%
NQC-KP	3	**28**	21	4
	5.4%	**50.0%**	42.0%	7.1%
KI-SB	7	23	**41**	7
	9.0%	29.5%	**52.6%**	9.0%
PI -SMI		1	6	**23**
		3.3%	20.0%	**76.7%**

OR-SQC = Oregon/northern California to southern Queen Charlotte Islands, NQC-KP = northern Queen Charlotte Islands to Kenai Peninsula, KI-SB = Kodiak Island to southern Bering Sea, PI-SMI = Pribilof Islands to St. Matthew Island

Table 4.8. Cross validation results of three category discriminant function classification for adult Pacific halibut (haul level) in the northeast Pacific based on parasite data. Numbers of fish assigned to category and the corresponding percentage of the sample in that category are shown. Correct classifications shown in bold (90% of 124).

	Assigned category		
True category	OR-SQC	SA1-PI	SMI
OR-SQC	**41**	4	2
	87.2%	8.5%	4.2%
SA1-PI	4	**67**	2
	5.5%	**91.8%**	2.7%
SMI			**4**
			100%

OR-SQC = Oregon/northern California to southern Queen Charlotte Islands, SA1-PI = southeast Alaska to Pribilof Island, SMI = St. Matthew Island

Table 4.9. Cross validation results of three category discriminant function classification for adult Pacific halibut (locality level) in the northeast Pacific based on parasite data. Numbers of fish assigned to category and the corresponding percentage of the sample in that category are shown. Correct classifications shown in bold (83% of 240).

	Assigned category		
True category	OR-SQC	NQC-SB	PI-SMI
OR-SQC	**6**	7	6
	82.9%	9.2%	7.9%
NQC-SB	10	**112**	12
	7.5%	**83.6%**	9.0%
PI-SMI		5	**25**
		16.7%	**83.3%**

OR-SQC = Oregon/northern California to southern Queen Charlotte Islands, NQC-SB = southeast Alaska to southern Bering Sea, PI-SMI = Pribilof Islands to St. Matthew Island

Table 4.10. Cross validation results of five category discriminant function classification for juvenile Pacific halibut in the northeast Pacific based on parasite data. Numbers of fish assigned to category and the corresponding percentage of the sample in that category are shown. Correct classifications shown in bold (43.5% of 62).

	Assigned category				
True category	NQC	KI	NI	UP	PI
NQC	**9**	4			
	69.2%	30.8%			
KI	1	**5**	1		
	14.3%	**71.4%**	14.3%		
NGI	5	3	**3**	2	
	38.5%	23.1%	**23.1%**	15.4%	
UP	5		2	**5**	1
	38.5%		15.4%	**38.5%**	7.7%
PI	6	4		1	**5**
	37.5%	25.0%		6.3%	**31.3%**

NQC = northern Queen Charlotte Islands, NI = Nagai Island, UP = Unimak Pass, and PI = Nunivak Island (central Bering Sea).

Table 4.11. Cross validation results of three category discriminant function classification for juvenile Pacific halibut in the northeast Pacific based on parasite data. Numbers of fish assigned to category and the corresponding percentage of the sample in that category are shown. Correct classifications shown in bold (66% of 62).

	Assigned category		
True category	NQC-NI	UP	PI
NQC-NI	**30**	3	
	90.9%	9.1%	
UP	6	**6**	1
	46.2%%	**46.2%**	7.7%
PI	10	1	**5**
	62.5%	6.3%	**31.3%**

NQC = northern Queen Charlotte Islands, NI = Nagai Island, UP = Unimak Pass, PI = Nunivak Island (central Bering Sea).

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CHAPTER 5 - THE EFFECT OF SPATIAL SCALE

Ecologists have come to view communities as the results of processes operating and interacting at various spatial and temporal scales. There is, further, an increasing awareness that the detection and interpretation of community patterns is dependent on the scale of the observations. Wiens and Rotenberry's series of papers in the early 1980s on shrubsteppe birds clearly indicated that patterns of habitat partitioning are scale-sensitive and that there are no clearly defined rules of habitat partitioning over several spatial scales (Rotenberry and Wiens 1980; Wiens and Rotenberry 1981; Wiens 1986). Levin (1992) argued that there was no single scale most appropriate for investigation.

Traditionally, community studies have focused on small scales to relate such processes as competition and predation to the observed patterns. There are many such examples in the literature (see Diamond and Case 1986 for a review). With respect to parasites, a classic example is Holmes' (1961) demonstration of distributional and size differences in parasites due to concurrent infections of acanthocephalans and cestodes in rats. The absence of such interactions in local studies of fish parasites (but see Bates and Kennedy 1990; Holmes and Bartoli 1993) has led parasitologists to view fish parasite communities as depauperate, isolationist assemblages that result from stochastic, supply-side processes (Kennedy et al. 1986; Kennedy 1990; but see Hartvigsen 1995).

A more recent, but less common and more difficult approach is to look for large scale patterns and processes that constrain or affect more local patterns. Island biogeography, for example, depends on regional influences to balance local processes. Regional patterns have been shown to be important determinants of local patterns in communities as disparate as freshwater fishes (Tonn 1990), Caribbean birds (Cox and Ricklefs 1977; Ricklefs and Cox 1978), cynipid wasps (Cornell 1985), and kelp (Dayton and Tegner 1984). Parasitologists have demonstrated the importance of large scale processes through the influence of host range (hosts with wider ranges have more parasites) (Price and Clancy 1983) and time since colonization of a locality by the host (more time in a locality results in more parasites) (Guégan and Kennedy 1993). But, the two known parasite studies (Aho 1990; Kennedy and Guégan 1994) that have made direct comparisons between local and regional patterns have concluded that regional patterns are only marginally important determinants of local

parasite community patterns.

The relative importance of processes operating at different spatial scales, although discussed since the fifties (Andrewartha and Birch 1954), has only recently received major attention. Levin (1992) (citing Whittaker 1975) reminds us that we cannot assume that communities are anything more than arbitrary collections of local species assemblages without assessing the relative importance of processes. Collins and Glenn (1990) concluded that for grassland plant communities the processes producing pattern at the regional scale are simply extensions of the processes producing pattern at the local scale. Hartvigsen (1995) argued that the scale of an investigation must be appropriate for the large scale processes under investigation.

In this chapter, I examine the relationship of patterns in the parasite communities of Pacific halibut at individual, local and regional scales. Specifically, I aim to determine: 1) if patterns at individual, local, and regional scales are related, 2) the extent of control by individual, local or regional processes, and 3) what the results tell us about processes organizing parasite communities in Pacific halibut and parasite communities in general.

MATERIALS AND METHODS

This study uses the 336 subadult/adult (>55 cm) fish from areas ranging from northern California to the Bering Sea. All fish from individual or closely adjacent hauls were assigned a haul number (Chapter 3: Table 3.1). A total of 206 adults from 13 individual or closely adjacent hauls each with a sample size of at least 10 fish comprises the data for the individual haul analysis. Localities are arbitrarily assigned (Chapter 3) and are composites of hauls in the same general area, including both fish from the hauls from the haul analysis and those fish from other hauls. Zoogeographic regions are those established in Chapter 3. Localities from California through the southern Queen Charlotte Islands are considered the southern region. Localities from the northern Queen Charlotte Islands to Kodiak Island are considered the central region. Localities west and north of Kodiak Island are considered the northern region.

Regional species richness (RSR) is defined as the total number of parasite species (all metazoans) in all fish taken from a given region. Local species richness (LSR) is defined as the total number of parasite species found in the sample of fish from an individual "haul" (LSRH) or "locality" (LSRL). The maximum number of taxa is the highest number of species found in any one fish from a sample (haul, locality, or region). The mean number of taxa is the average number of species per fish in any sample or aggregation of samples. Species referred to as common are those present in at least 50% of the fish in a sample. Species referred to as uncommon are those present in 25-49% of a given sample. Rare species are those present in less than 25% of individuals in a sample. The complement of Simpson's Index (1-D) is used as the index of diversity. Evenness is expressed as $((1\text{-}D)\text{-}(1\text{-}D_{min})/((1\text{-}D_{max})\text{-}(1\text{-}D_{min}))$ following Krebs (1992).

Niche occupation patterns of gastrointestinal species were examined using the frequency distribution of empty sections and the Overlap Index of Hurlbert (1978). Fisher's Exact Test (adjusted for an experimentwise error rate with the Dunn-Šidák method (Sokal and Rohlf 1981)) was used to test for negative cooccurrences among pairs of parasites that overlapped at least 25% in their distributions.

Standard linear regression, Spearman correlation, ANOVA, and nested ANOVA techniques were used to investigate the effects of scale and the relationship between scales. Effects of potentially correlated variables such as sampling effort ($\log_e$ number of fish sampled), halibut biomass, and fish size were examined and, if necessary, controlled using partial correlations. In regression analysis, I fit untransformed, exponential,

and power function models, choosing the best fit by visual inspection, inspection of residuals, r^2, and examination of F-test values. For the nested ANOVAS, since theoretical distributions of diversity and evenness values are not clearly known, results from both untransformed and ln (x+1) transformed values were examined. Statistical analyses were performed in SYSTAT for Windows version 5.05 (Wilkinson 1992) and SPSS for Windows 95 version 7.0 (Norušis 1995). Diversity and evenness measures were calculated for each fish in INFRACOM, a shareware program by A. W. Shostak (1992). In instances in which the combination of a low number of both species and individuals and rounding error caused the Krebs formula to provide a poor estimate of evenness (i.e. negative evenness or evenness greater than 1), evenness was calculated by hand.

RESULTS

Regional species richness is lowest in the southern region (Table 5.1) and similar in the central and northern regions, though the species comprising RSR are not the same (see Chapter 3). The maximum number of taxa in any individual fish is highest in the central region, and similar in the southern and northern regions (Table 5.1). Fish from the southern region had significantly more parasites, but the infracommunities were characterized by fewer species, lower diversity and evenness (Table 5.1).

At the locality level, there are both more taxa and higher maximum numbers of taxa in localities associated with the central region (Table 5.2). There are significant differences in parasite number, species number, diversity, and evenness among the localities (Table 5.2). The general pattern for the region is also shown in almost all localities in that region. These values are not correlated with sample size. Overall, the number of species is positively correlated with worm number and diversity and evenness are negatively correlated with worm number. Within individual localities, the number of species usually is not correlated with worm number, but diversity and evenness are consistently negatively correlated with worm number.

Patterns in individual hauls largely reflect those at the locality level. There are more taxa and a higher maximum number of taxa in localities associated with the central region. There are significant differences in parasite number, species number, diversity, and evenness among the hauls (Table 5.3). These values are not correlated with sample size. Overall, the number of species is positively correlated with worm number, but diversity and evenness are negatively correlated with worm number. Within individual hauls the number of species usually is not correlated with worm number, but diversity and evenness are generally negatively correlated with worm number.

Nested ANOVAS for total parasite number (log), species number, diversity, and evenness show that most of the variation is accounted for by differences among individual fish (Table 5.4). For the number of parasites, region and locality are significant factors. Only locality is significant for diversity and none of the factors for evenness, though locality approaches significance for evenness. Haul and region are important for species number.

Regional species richness of GI parasites is lowest in the southern region and highest in the northern region (Table 5.5). The maximum number of taxa is similar in all regions. The southern region has

significantly more parasites and the northern region has a significantly lower average number of species. There are no significant differences in diversity or evenness patterns.

Locality patterns in GI parasites show much variability, but no obvious trends among localities with respect to the number of species (Table 5.6). There is much similarity among localities in the maximum numbers of taxa. There are significant differences in parasite number, average number of taxa, diversity, and evenness. Only the pattern in the average number of species matches the regional pattern. These values are not correlated with sample size. Overall, as in the previous analyses, the number of species is positively correlated with worm number. Diversity and evenness are negatively correlated with worm number. Within individual localities, however, there are few correlations among species number, worm number, diversity, or evenness. The correlations that do exist follow the same pattern of positive correlations between the number of species and parasite number and negative correlations between diversity and parasite number and evenness and parasite number. The correlations between diversity and evenness and parasite number appear to be more common in southern localities.

At the haul level, there is considerable variability in the number of species, but general similarity in the maximum number of species among the hauls (Table 5.7). Southern hauls have significantly more parasites, a reflection of the regional pattern. There is a significant difference in the average number of taxa among hauls, but with no identifiable gradient. There are no significant differences in diversity or evenness among hauls. These values are not correlated with sample size. Again, the number of species is positively correlated with worm number and diversity and evenness are negatively correlated with worm number. Within individual hauls, there are few correlations among species number, worm number, diversity, or evenness, but those that do exist follow the same pattern. The correlations between diversity and evenness and parasite number appear to be more common in southern localities.

Nested ANOVAS for GI parasites show essentially the same patterns as for total parasites (Table 5.8). Region and locality are significant factors for the number of parasites (log) and number of species (locality is only marginally significant here). Only locality is significant for diversity and none are significant for evenness.

Similarity analysis reveals that similarities are highest within hauls (percentage similarity (PSIM) =

0.460 ± 0.042, Jaccard's coefficient (JAC) = 0.465 ± 0.022. Similarities within localities (PSIM = 0.442 ± 0.042, JAC = 0.447 ± 0.022) are higher than similarites within region (PSIM = 0.330 ± 0.054, JAC = 0.408 ± 0.020).

Local species richness at the haul level (LSRH) averages 64.4% of RSR. LSRH is positively related to RSR, but only marginally so; only about 27% of the variation is explained in the relationship ($p = 0.068$). However, when the effects of halibut biomass (Table 5.9) and sample size are controlled using partial correlations, a different pattern emerges. The correlation between LSRH and RSR with sample size controlled is not significant ($p = .15$, $r^2 = 0.181$). With sample size controlled, LSRH is significantly correlated with biomass ($p = \sim.02$). Controlling for biomass produces no significant correlations among sample size, LSRH, and RSR. Therefore, halibut biomass appears to be a better predictor of LSRH than either sample size or RSR. LSRH of common species is relatively stable and not correlated with RSR ($p = 0.631$, $r^2 = 0.022$), but the proportion of uncommon species in LSRH increases significantly with RSR ($p = 0.03$, $r^2 = 0.036$).

At the locality level, there is no relationship between RSR and LSRL ($p = 0.441$, $r^2 = 0.05$). LSRL averages 71.5% of RSR. The relationship is still positive, but no longer significant.

Analysis of niche occupation patterns in gastrointestinal helminths reveals considerable empty space. Seventy percent of the hosts have at least half of the intestinal sections empty (Figure 5.1). Niche overlap analysis shows that most parasites either overlap completely in their distributions or hardly at all (Table 5.10). Co-occurrence analysis among pairs of parasites (in those localities where both species are present) whose distributions overlap at least 25% reveals no significant negative co-occurrences after a Dunn-Šidák adjustment for an experimentwise error rate (Table 5.10).

DISCUSSION

Most studies of the parasite communities in poikilotherms have examined single scale phenomena and some have successfully identified processes that are capable of producing the observed patterns. At small spatial scales the focus has traditionally been on stochasticity (Kennedy 1990; McDowell et al. 1992; Kennedy and Guégan 1994), but Bates and Kennedy (1990) and Holmes and Bartoli (1993) identified potential interactive structuring mechanisms at the infracommunity level. At larger scales, the focus has been on biogeographic factors (Kennedy 1978; Marcogliese and Cone 1991), phylogenetic constraints (Leong and Holmes 1981; Kennedy and Bush 1994), and energy flow (Wisniewski 1958; Esch 1971). The "missing link" to date has been an absence of an examination of the extent to which patterns at the regional level influence patterns at successively smaller scales. Aho (1990) and Kennedy and Guégan (1994) admit the role of large scale processes in setting boundaries, but do not believe they significantly impinge upon local stochasticity. However, the successful use of parasites as biological tags implies important large scale patterns that should influence local patterns. Hartvigsen (1995), in one of the only examinations of the importance of multiple scales in parasite communities, argues that it is crucial to capture the regional dynamics of a system in order to properly scale the interpretations of local patterns. Indeed, she suggested that the conclusions of some previous "local process" studies (Kennedy 1977, 1978a, 1978b) are insupportable due to improper scaling.

Individual fish

The most natural scale is that of the infracommunity, the parasites of an individual fish. It is at this level that parasites establish, live, potentially interact, and reproduce. Processes that determine the number and nature of these parasites are often associated with individual fish. My results show that the most important contributor to overall variation is variation among individual fish. A substantial portion of this variation is associated with the size and growth rate of the host (Chapter 2). Larger fish grow faster; thus, they eat more and are exposed to more parasites. They may also be able to harbor more parasites without being harmed (Chapter 2).

Stochasticity also appears to play a large role, as evidenced by the high variances associated with fish collected at the same time and place (haul). This variation supports the idea that local "noise" is important in

parasite communities (Kennedy and Bush 1994), and suggests that halibut appear to be random samplers of what is available to them. This variation may be constrained in at least two ways, through interactions among parasites, or through specificity.

Ricklefs (1987) noted that ecologists often assume that local species abundance patterns are the outcome of deterministic local processes, including interactions. According to Ricklefs (1987), all hypotheses based solely on local-processes predict 1) community convergence, 2) resistance of the community to invasion, and 3) no relationship between local and regional richness. He concludes that many studies fail to show these patterns. My data do not support any of these patterns. The variability among individual fish and in local species richness across the range of halibut suggests no convergence. The amount of empty space, the varying number of rare species overlaying a baseline of common species, and the lack of apparent interactions all suggest that my system is amenable to invasion. My data at the haul level show a strong relationship between regional richness (total number of species) and average infracommunity richness. Thus local interactions do not appear to be important constraints on halibut parasite infracommunities.

Although most of the parasites found in halibut are generalists, there is a complement of species specific to, or with a predilection for, pleuronectids, and these include several of the common parasites (Chapter 2). In addition, the parasite community in halibut resembles those of other flatfishes much more than it resembles those of other piscivores (Chapter 2). Thus host specificity does play a role in determining halibut infracommunities.

Hauls

The next scale is that of a haul, which is the closest representation of a group of fish from a single location available in my study. Given the mobility, range, and lack of territoriality of halibut, each fish should have access to the entire area sampled and should be exposed to the same complex of parasites. Indeed, similarities within hauls are significantly higher than those within localities. In addition, clustering of individuals (Chapter 3) suggested that some hauls are unique.

However, the ANOVAs suggest that variation at this scale is relatively unimportant, contributing significantly only to variation in the number of species. This is despite the fact that variability in depth, which

does affect both the number of species and the number of individual parasites (Chapter 3), is included at this scale. In part, the insignificant contribution of variation at this scale may be an artifact, due to the very uneven sample sizes of different hauls, and the differences in numbers of hauls per locality. Both are unavoidable consequences of the material available to me.

Localities

This scale represents a summary of all fish from an arbitrary geographical region. It represents a spatial scale intermediate between the "point source" of a haul and the biologically defined region. It is probably too large for fish to have equal access to all of it. It was used as the basis for the zoogeographical analysis because of the larger and more equitable sample sizes.

Variation at the scale of locality is the second most important contributor (after individual fish) to variation in diversity, for both all parasites and GI parasites. It is a significant contributor, but ranking behind individual fish and region, to variation in number of parasites (both data sets) and number of species (GI parasites).

One pattern apparent at both haul and locality scales, and both among and within units at each scale, is that both diversity and evenness are negatively correlated with parasite number. This strongly suggests that throughout their eastern Pacific range, halibut increase numbers of the more common species much faster than they increase numbers of the less common species, or add new species. This pattern provides further support for the importance of specificity.

Differences among localities may include variability in the composition and/or abundance of intermediate host communities and may be created by current and oceanographic patterns, differences in productivity, and differences in the assemblages of other organisms. At this level, the differences that create pattern in the parasite community also may produce differences in the halibut community. Halibut biomass does appear to be a significant determinant of the parasite community structure in halibut. Local richness is positively correlated with biomass. A larger biomass indicates a richer community and richer communities may support a greater variety of parasites. The correlation with biomass may also indicate that halibut expand their diet as populations increase, and therefore acquire different parasites.

Regions

This level represents the widest spatial scale identified in this study and is based on the results of the zoogeographic analysis (Chapter 3). Variation at this scale is the second most important contributor (behind individual variation) to species number and parasite number for both total parasites and GI parasites. The consistently high proportion of regional richness represented in local richness (at either the haul or locality level) is also suggestive of the importance of regional processes. An examination of regional community patterns suggests that there is a maximum limit imposed on the parasite fauna. There are more parasites, but fewer species and lower diversity and evenness values in the south. It therefore appears that there is a trade off between dominance in abundance and dominance in richness. The mechanism through which this operates is unclear. Because the pattern is not apparent at smaller scales, it is unlikely to be due to interactions. Rather, it is most likely to be due to biogeographic processes.

Processes

Biogeography is an important process producing pattern in my study. The various parasite species have their particular, independent ranges, thus creating clinal variation in the parasite fauna of halibut. Some species, however, have more restricted ranges and thus superimpose a pattern on the overall clinal one. Temperature is associated with biogeography and probably plays a large role in determining distributions. Increased temperature in the south also appears to contribute to the increase in abundance of parasites. In addition, the lower richness in the south may be related to the narrower continental shelf, which may restrict populations of intermediate host species.

Niche expansion also appears to play an important role in producing pattern in my system. I found that species richness is correlated with halibut biomass. Halibut may increase their niche breadth when (or where) populations are high and, as a result, acquire more, different kinds of parasites. Alternatively, higher populations of halibut may support more species of parasites. I believe the alternative explanation is unlikely because most of the halibut parasites are generalists and, therefore would not specifically track halibut populations. Rather, they would track general community richness, which is not necessarily correlated with halibut abundance.

I believe that both host specificity and the exchange (or sharing) of parasites among several host species are important processes in my system. Host specificity is important because it provides a baseline parasite community. Exchange is important because it supplements the baseline community. Exchange is pervasive due to two factors: the nature of the marine system, in which parasites exploit multiple pathways to completing their life cycles, and the breadth of the halibut's diet.

The breadth of the halibut's diet is an important factor. The ontogenetic changes in the halibut's life history provide the framework around which the parasite community assembles and changes. The parasite communities in small fish are relatively depauperate and reflect the largely invertebrate diet. Likewise, the variety and substantial number of parasites in adults reflects their piscivorous, but still opportunistic, diet.

Feeding rate is even more important. I showed that those fish that have grown faster have more parasites, probably because they have eaten more and been exposed to more parasites. Temperature may also influence feeding rate since metabolic processes increase at higher temperatures. This may be a particularly important process in southern fish and may explain the increased parasite abundance in the south.

I have shown that halibut harbor a richer, more abundant parasite fauna than most other marine fishes, making regulatory processes more likely. However, the only patterns suggestive of any regulatory process are the relatively constant number of common species throughout the northeast Pacific and the apparent trade-off of richness and abundance in the south. Neither are explicable by any pattern at the infracommunity level, suggesting that any such regulatory process must act at a larger scale. Just what that process might be, or at what scale it might operate, are not at all clear. In addition, it is possible that there are some processes that may limit or prevent the development of some parasites in halibut. Those processes, though there is little evidence of them, are also unexplored.

Finally, stochasticity is critical. All of the above processes (except specificity) suggest that the system is controlled by supply-side (exposure) limitations or recruitment limitations (development). There is no evidence for any important post-recruitment processes; therefore, the pattern in the community is determined by what parasites are available and which of those parasites are able to develop in halibut. Which parasites get into the host is determined by individual feeding habits of halibut. Which parasites develop may be due to a halibut's ability to harbor the parasite (particularly the non-specific ones), which may include variability in

susceptibility among individual halibut (Anderson 1982).

In conclusion, it is certain that no single process produces the patterns observed in the parasite communities of halibut at any spatial scale. Rather, there is a complex interaction of processes at many spatial scales. Biogeography may provide a potential fauna, but the size/age, feeding rate, and susceptibility of individual halibut in combination with halibut population levels and parasite specificity determine which and how many parasites are likely to be found in an individual halibut. Moreover, these processes are not limited to determining halibut parasite communities. These processes are likely to be involved in shaping the parasite communities in all marine fishes (or any marine animal), though the individual characteristics of each species may influence the relative importance of these various processes.

Table 5.1. Community measures (± SD) for the parasite infracommunities of Pacific halibut at the regional level. Groupings of localities within the region are given in parentheses. P-values denote statistical significance of differences in values among regions (Kruskal-Wallis).

Region	n	Ave. No. Parasites	No. taxa	Max. taxa	Ave. Taxa	Ave. 1-D	Ave. Evenness
South (OR-SQC)	100	494±437	39	17	10.9±2.3	0.49±0.18	0.52±0.20
Central (NQC-KP)	79	235±190	48	22	13.4±3.2	0.64±0.19	0.61±0.19
North (KI-SMI)	157	210±219.2	49	18	11.5±2.39	0.59±0.22	0.61±0.24
p		<0.001			0.039	<0.001	0.002

OR = Oregon, WA = Washington, VI = Vancouver Island, SQC = southern Queen Charlotte Islands, SA1 = southeast Alaska 1, SA2 = southeast Alaska 2, KP = Kenai Peninsula, KI = Kodiak Island, NI = Nagai Island, UP = Unimak Pass, WAL = western Aleutian Islands, SB = southern Bering Sea, PI = Pribilof Islands (central Bering Sea), SMI= St. Matthew 's Island

Table 5.2. Community measures (± SD)for the parasite infracommunities of Pacific halibut at the locality level. Locality abbreviations are as in Table 5.1. The corresponding region for the locality is given in parentheses. P-values denote statistical significance of differences in values among localities (Kruskal-Wallis).

Locality (region)	n	Ave. No. Parasites	No. Taxa	Max. Taxa	Ave. Taxa	Ave. 1-D	Ave. Evenness
OR (S)	23	670±634.0	33	16	11.7±2.32	0.48±0.21	0.51±0.22
WA (S)	14	454±327.8	27	16	12.1±2.21	0.54±0.19	0.56±0.22
VI (S)	32	589±430.4	31	14	10.5±2.11	0.45±0.17	0.48±0.19
SQC (S)	31	284±134.3	32	17	10.4±2.34	0.51±0.15	0.54±0.18
NQC (C)	8	235±151.9	24	14	11.4±1.51	0.6±0.07	0.62±0.08
SA1 (C)	20	309±258.6	38	20	12.5±2.86	0.55±0.18	0.57±0.2
SA2 (C)	30	227±191.8	44	22	14.3±3.3	0.64±0.23	0.65±0.25
KP (C)	21	177±90.0	35	20	13.8±3.5	0.74±0.12	0.76±0.13
KI (N)	26	160±103.9	38	17	13.2±2.47	0.71±0.15	0.74±0.18
NI (N)	14	193±106.0	28	14	10.5±1.99	0.61±0.14	0.65±0.16
UP (N)	20	190±186.3	36	15	11.5±1.57	0.53±0.20	0.53±0.23
WAL (N)	21	194±231.5	36	18	11.7±2.47	0.59±0.24	0.6±0.26
SB (N)	31	347±344.0	34	17	11.3±2.68	0.45±0.23	0.46±0.25
PI (N)	14	232±208.2	25	14	11±2.32	0.56±0.23	0.58±0.27
SMI (N)	15	135±113.3	37	15	11.1±2.07	0.65±0.19	0.66±0.23
p		<0.001			<0.001	<0.001	<0.001

Table 5.3. Community measures (± SD) for the parasite infracommunities of Pacific halibut at the haul level where n ≥ 10. Haul abbreviations are as in Table 5.1. The corresponding region for the haul is given in parentheses. P-values denote statistical significance of differences in values among hauls (Kruskal-Wallis).

Haul	n	Ave. No. Parasites	No. Taxa	Max. Taxa	Ave. Taxa	Ave. 1-D	Ave. Evenness
OR (S)	10	611±515.1	28	16	11.8±2.39	0.47±0.24	0.49±0.25
WA (S)	10	432±315.8	28	15	12.1±1.85	0.51±0.21	0.52±0.23
VI (S)	20	581±420.6	25	14	10±2.38	0.42±0.17	0.45±0.19
SQC (S)	31	284±134.3	31	17	10.4±2.34	0.51±0.15	0.54±0.18
SA1 (C)	10	283±227.3	31	20	12.2±3.19	0.59±0.17	0.62±0.19
SA2 (C)	15	218±134.9	39	22	14.7±3.40	0.64±0.22	0.65±0.25
KP (C)	21	177±90.0	35	20	13.8±3.50	0.74±0.12	0.76±0.13
KI (N)	14	174±131.7	30	17	12.2±2.59	0.71±0.14	0.75±0.17
NI (N)	14	193±106.0	28	14	10.5±3.96	0.61±0.14	0.65±0.16
WAL (N)	20	194±276.1	36	18	11.7±2.54	0.60±0.28	0.61±0.3
SB (N)	20	383±379.2	33	17	12.3±2.59	0.48±0.23	0.49±0.23
PI (N)	11	248±232.0	24	14	11.1±2.55	0.51±0.24	0.52±0.28
SMI (N)	10	110±43.4	30	13	10.3±1.71	0.76±0.05	0.80±0.06
p		<0.001			<0.001	<0.001	<0.001

Table 5.4. Proportion of variation in community measurements in individual Pacific halibut associated with different spatial scales. Data presented are the results of a nested ANOVA.

Measure	n	F (adjusted)	p	Proportion of variation (%)
Parasite number (log)				
region	3	11.179	0.001	23.8
locality	15	5.313	0.027	5.5
haul	34	0.579	0.920	0
individuals (within haul)	336			70.6
Species number				
region		5.301	0.021	11.3
locality		1.302	0.317	2.7
haul		1.687	0.037	7.7
individuals (within haul)				78.4
Diversity				
region		1.537	0.251	2
local		3.176	0.034	11.9
haul		1.038	0.417	0.7
individuals (within haul)				
Evenness				
region		1.087	0.366	0.4
local		2.310	0.08	9.6
haul		1.272	0.2	3.8
individuals (within haul)				86.5

Table 5.5. Community measures (± SD) for GI parasites of Pacific halibut by region. Abbreviations are as in Table 5.1. Locality groupings for the region are given in parentheses. P-values denote statistical significance of differences in values among regions (Kruskal-Wallis).

Region	n	Ave. No. Worms	No. Taxa	Max. Taxa	Ave. Taxa	Ave. 1-D	Ave. Evenness
South (OR-SQC)	100	224±344	15	9	4.0±1.4	0.37±0.23	0.45±0.32
Central (NQC-KP)	79	136±179	17	9	4.0±1.8	0.37±0.23	0.45±0.35
North (KI-SMI)	157	116.5±220.2	20	8	3.2±1.45	0.33±0.26	0.41±0.48
p		<0.001			<0.001	0.295	0.507

Table 5.6. Community measures (± SD) for GI parasites of Pacific halibut at the locality level. Locality abbreviations are as in Table 5.1. The corresponding region for the locality is given in parentheses. P-values denote statistical significance of differences in values among localities (Kruskal-Wallis).

Locality	n	Ave. No. Worms	No. Taxa	Max. Taxa	Ave. Taxa	Ave. 1-D	Ave. Evenness
OR (S)	23	379.2±444.1	10	6	4.0±1.28	0.33±0.26	0.39±0.34
WA (S)	14	257.9±304	9	7	4.6±1.39	0.37±0.24	0.43±0.29
VI (S)	32	232.5±393.2	12	7	3.9±1.23	0.35±0.22	0.45±0.31
SQC (S)	31	86.8±92.8	14	9	3.7±1.47	0.42±0.22	0.51±0.34
NQC (C)	8	117.9±122.7	5	5	2.3±1.17	0.19±0.15	0.31±0.28
SA1 (C)	20	181.4±235.3	12	7	3.5±1.47	0.26±0.18	0.35±0.28
SA2 (C)	30	141.3±194	16	9	4.4±2.1	0.40±0.25	0.45±0.34
KP (C)	21	93±94.6	12	7	4.5±1.4	0.48±0.17	0.61±0.42
KI (N)	26	67.5±50.8	14	6	3.8±1.22	0.40±0.20	0.61±0.80
NI (N)	14	54.4±48.7	10	5	2.6±1.02	0.38±0.24	0.48±0.38
UP (N)	20	87.7±193.5	14	4	2.5±1.28	0.27±0.28	0.27±0.14
WAL (N)	21	118.1±239.2	14	6	3.2±1.55	0.40±0.25	0.49±0.38
SB (N)	31	267.1±353	13	8	3.2±1.72	0.19±0.25	0.19±0.30
PI (N)	14	135.7±222.2	8	5	2.7±1.14	0.26±0.26	0.35±0.39
SMI (N)	31	43.9±87	16	6	3.5±1.39	0.44±0.24	0.49±0.43
p		<0.001			<0.001	<0.001	0.017

Table 5.7. Community measures (± SD) for GI parasites of Pacific halibut at the haul level. Haul abbreviations are as in Table 5.1. The corresponding region for the haul is given in parentheses. P-values denote statistical significance of differences in values among hauls (Kruskal-Wallis).

haul	n	Ave. No. Worms	No. Taxa	Max. Taxa	Ave. Taxa	Ave. 1-D	Ave. Evenness
OR (S)	10	345±537	9	5	4.2±0.92	0.41±0.26	0.47±0.38
WA (S)	10	260.9±353.7	8	7	4.5±1.40	0.43±0.25	0.50±0.30
VI (S)	20	263.2±482.5	9	5	3.5±0.95	0.35±0.23	0.46±0.32
SQC (S)	31	86.8±92.8	14	9	3.7±1.47	0.42±0.22	0.51±0.34
SA1 (C)	10	128.5±110.3	9	7	3.3±1.64	0.29±0.17	0.42±0.31
SA2 (C)	15	132.4±145.2	14	8	4.5±2.07	0.42±0.25	0.45±0.37
KP (C)	21	93±94.6	12	7	4.5±1.4	0.48±0.17	0.61±0.42
KI (N)	12	65.6±45.8	9	6	3.7±1.07	0.42±0.17	0.83±1.09
NI (N)	14	54.4±48.7	10	5	2.6±1.02	0.38±0.24	0.48±0.38
UP (N)	20	123.5±244.1	14	6	3.3±1.56	0.39±0.26	0.47±0.38
SB (N)	20	291.8±389.2	12	8	3.7±1.66	0.22±0.27	0.19±0.26
PI (N)	11	155.5±247.2	7	5	2.7±1.27	0.25±0.28	0.32±0.38
SMI (N)	10	30.8±26.7	11	6	3.7±1.64	0.44±0.31	0.53±0.41
p		0.028			0.002	0.098	0.104

Table 5.8. Proportion of variation in community measurements in gastrointestinal parasites of individual Pacific halibut associated with different spatial scales. Data presented are the results of a nested ANOVA.

Measure	n	F (adjusted)	p	Proportion of variation
Parasite number (log)				
region	3	5.93	0.013	14.8
locality	15	8.72	0.021	7.9
haul	34	0.49	0.966	0
individuals (within haul)	336			77.1
Species number				
region		4.09	0.041	10.6
locality		2.68	0.053	9.5
haul		1.17	0.284	1.8
individuals (within haul)				77.9
Diversity				
region		0.02	0.979	0
locality		11.19	0.02	10.6
haul		0.46	0.977	0
individuals (within haul)				88.9
Evenness				
region		0.14	0.993	0.05
locality		3.68	0.093	3.9
haul		0.66	0.764	0
individuals (within haul)				96.4

Table 5.9. Total exploitable biomass estimates for Pacific halibut by locality (Sullivan and Parma 1995). Abbreviations are as in Table 5.1.

Locality	Total exploitable biomass (million pounds)
OR	3.6
WA	3.6
VI	3.6
SQC	60.5
NQC	72
SA1	72
SA2	161.6
KP	161.6
KI	161.6
NI	40
UP	40
WAL	36.1
SB	36.1
PI	36.1
SMI	36.1

Table 5.10. Overlap and cooccurrence among gastrointestinal parasites of Pacific halibut with at least 25% overlap in distribution. The bottom half of the table contains the Overlap Index and the top half contains Fisher's Exact Probability of negative coocurrences . α' (Dunn-Šidák method) = .003

Fisher's Exact Probability

Overlap Index

	Bracre	Capmar	Dervar	Dislae	Gonphy	Hemlev	Parpar	Podgib	Probar	Scopli	Tublin
Bracre	-		0.18			0.80	0.09				0.18
Capmar		-						0.12		0.02	
Dervar	0.96		-	1.0	0.52	0.82	0.11				0.25
Dislae			0.99	-							0.47
Gonphy			1.0		-						1.0
Hemlev	1.0		1.0			-					0.007
Parpar	0.93		0.80				-				0.07
Podgib		0.4						-		0.08	
Probar									-	0.10	
Scopli		0.25						0.25	0.68	-	
Tublin	0.97		0.98	1.0	1.0	1.0	0.9				-

Bracre = *Brachyphallus crenatus*, Capmar = *Capillaria margolisi*, Dervar = *Derogenes varicus*, Dislae = *Dissosaccus laevis*, Gonphy= *Gonocerca phycidis*, Hemlev = *Hemiurus levinseni*, Parcap = *Paracapillaria parophrysi*, Podgib = *Podocotyle gibbonsia*, Probar = *Prosorhynchoides basargini*, Scopli = *Scolex pleuronectis (intestinal form)*, Tublin = *Tubulovesicula lindbergi*

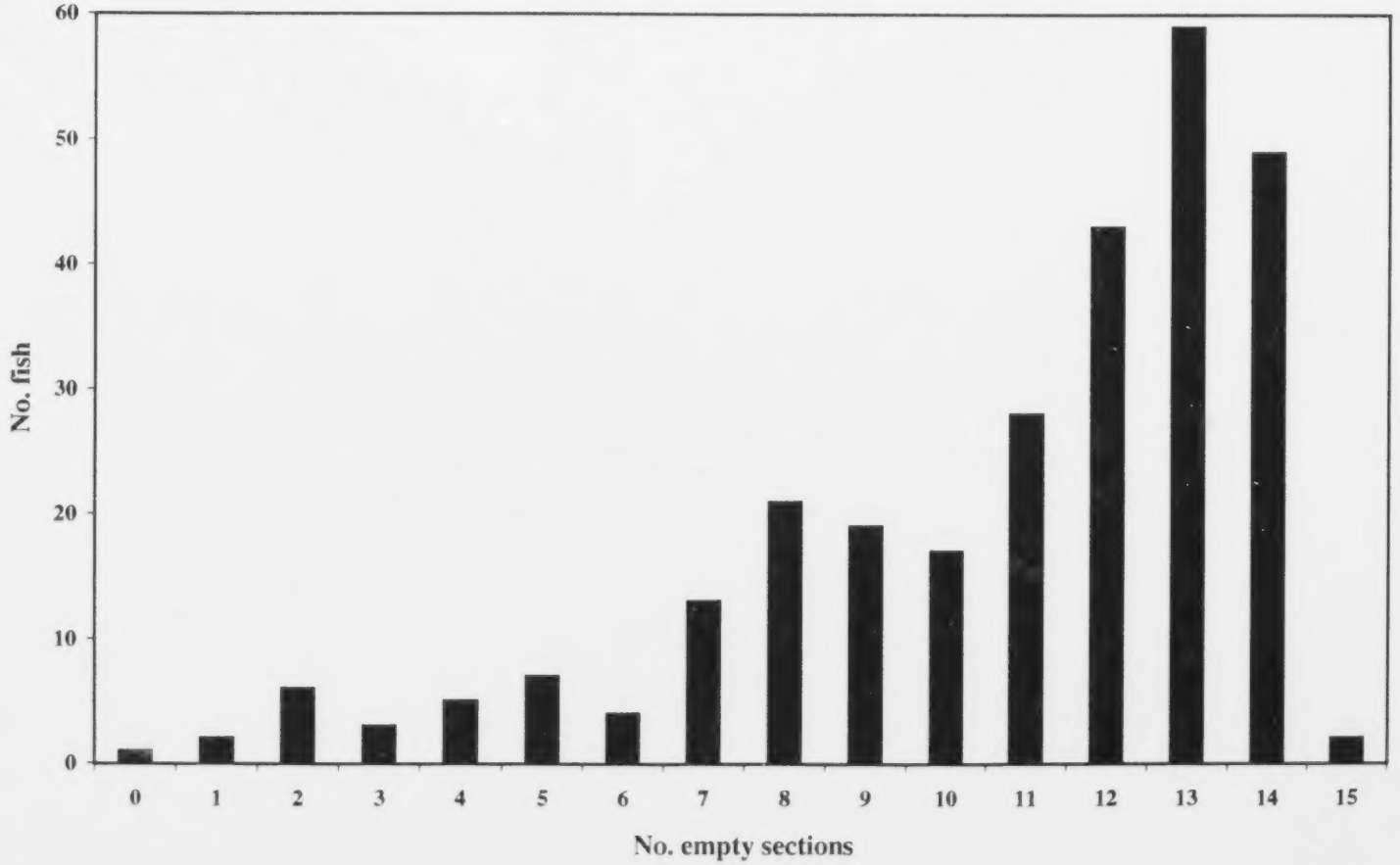

Figure 5.1. Distribution of the number of empty intestinal sections in 336 adult Pacific halibut, *Hippoglossus stenolepis*.

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CHAPTER 6 - GENERAL DISCUSSION

Parasites exist along a continuum of ecological scales. The processes through which the parasites are assorted vary depending on the temporal or spatial scale being examined. Levin (1992) points out that there is no single scale most appropriate for ecological investigation. Therefore, an examination from several perspectives is necessary to begin to understand the organizing principles in a community.

In this thesis I have examined the parasite assemblage in Pacific halibut at various spatial and temporal scales from the perspective of both ecology and fisheries management with the dual objectives of identifying basic ecological patterns and using those patterns to address applied questions. In this chapter I will review my findings and the extent to which the objectives have been addressed.

Clearly, and not unexpectedly, the patterns I found are amalgams of properties resulting from several processes (Chapter 5). Ultimately, large scale zoogeographic processes determine the pool of parasites available in a locality. The ability to identify zoogeographic regions (Chapter 3) attests to this. However, it is also clear that, because of fish movements and the complex overlapping distributions of intermediate hosts, sharp boundaries cannot be drawn. Large scale patterns are significant enough and movement of adult fish is limited enough, however, to allow some degree of stock differentiation (Chapter 4). The pool of available species is modified locally based on local conditions. Characteristics of the host species also influence the effect of locality. Halibut biomass appears to influence species richness, probably through diversification of feeding habitats in the presence of increased competition from other fish. This also suggests regional enrichment because the supply of potential colonists (parasites maintained by other species of fish in the area) does not appear to be limiting. The supply of colonists accounts for the relationship between rare species and regional richness. Hauls do have some unique characteristics, indicating that the patchiness in the system occurs at a scale smaller than locality. Variation among individual fish taken at the same time and place accounts for a great deal of the variation observed in parasite infracommunites (Chapter 5). Thus, patterns are nested within much ecological 'noise' as Kennedy and Bush (1994) hypothesized.

Within individuals, growth rate and ontogenetic niche shifts appear to be the primary determinants in the development of the assemblage. Host characteristics determine which species from the local pool are likely

to be represented and growth rate (presumably operating through feeding rate) determines how many individuals are present. Parasite specificity may predispose some parasites for occurrence, but ecological factors determine their acquistion (Chapter 2). Thus, even though different species of flatfish tend to have similar parasites, their presence in any individual fish seems largely controlled by chance because variation among individual fish explains most of the variability in the community. The assemblage appears to be basically stochastic, not interactive. The size and number of the parasites in relation to the size of the host environment and the lack of negative coocurrences suggests little opportunity for interaction (Chapter 5).

Parasites do appear to have a negative impact on halibut. The smallest fish in the 5, 6, and 7 year age-classes may have growth rates depressed, and appear to be lost from the population (Chapter 2). However, there is little evidence that parasites contribute to mortality in larger fish. Some parasites also may have a negative impact on the marketing of halibut. Myxosporea relevant to the marketing of halibut include *Unicapsula muscularis* and *Kudoa thyrsites*. *Unicapsula* is the reported cause of "wormy" halibut (Thompson 1916; Davis 1923). The parasite fills and distorts muscle fibers so that they appear wormlike. Thompson (1916) refers to the condition as "rare" and notes that the host specimens were in poor condition when examined. Between 1916 and the time of my study, there were no reports of the parasite. In my study the parasite is more common than Thompson's study implies (he does not provide prevalence data). In fact it is probably more common than I report. The small size of the individual organisms and the inconspicuousness of the pseudocysts make *Unicapsula* difficult to identify, particularly in fresh fish. I found that as flesh quality decreases with storage time, the pseudocysts, which otherwise may look like connective tissue, become more obvious. Therefore, minimizing storage time should prevent this problem.

Patashnik and Groninger (1964) identified *Kudoa* as the cause of "milky" flesh in about 0.3% of 3 landings of halibut in 1961. I found *Kudoa* in about 25% of the overall sample, but spotty in distribution. Further, I found *Kudoa* in only 3% of adult fish. *Kudoa* appears to be more common in the Gulf of Alaska area and absent from localities both west of Unimak Pass and from the Bering Sea. With respect to soft flesh and pockets of liquefied tissue, however, I found them in 1% or less of the sample. Therefore, marketable fish are much less likely to be infected and the presence of the organism is not necessarily indicative of a flesh quality

problem. Evidence from Atlantic salmon suggests that soft flesh only occurs after a threshold density of parasites is reached (M. L. Kent, DFO, personal communication). Freezing is apparently not related to the occurrence of soft flesh. In my study, there was no association between storage time and the presence of *Kudoa* associated soft flesh. Neither was there a relationship between the prevalence of the organism and storage time. Given the low prevalence of the infection and the even lower incidence of soft flesh, *Kudoa* is not likely to present a significant marketing problem.

Helminths relevant to the marketing of halibut include the larval nematodes *Anisakis simplex* and *Pseudoterranova decipiens*, both of which are infective to humans. *Anisakis* is one of the most common and abundant parasites of halibut. Worms are located primarily in the mesenteries and belly flaps. The current practice of discarding belly flaps helps alleviate this problem. However, prevalence and intensity increases dramatically with host size. This increases the likelihood that worms will be found in the surrounding flesh. *Pseudoterranova* is a large, brownish worm found in the belly flaps and surrounding tissue. Prevalence increases with host size, but intensity does not. Proper freezing and/or thorough cooking prevents transmission of both parasites to humans.

The success of the discriminant function analysis (Chapter 4) suggests that it may be desirable to manage southern fish separately from northern fish. My results also suggest mixing in juveniles from the different areas, though conclusions are less clear than in adults due to low prevalence and abundance of parasites. This portion of the study highlighted the interplay of pure and applied science. Patterns identified in the zoogeographic analysis (Chapter 3) did not completely match those identified in the stock discrimination analysis. These differences are influenced by the nature of the questions asked, but complement one another. The use of many short-term parasites in the zoogeographic patterns allowed considerable insight into parasite zonation, but the successful use of long-term parasites to identify groups of fish indicated that by focusing on a slightly larger spatial scale and a longer temporal scale, different, but equally valuable, questions could be answered.

In conclusion, this study unites pure and applied science. Because Pacific halibut is a commercially important species, support provided by the IPHC allowed me the opportunity to examine a host over virtually

all its vast range, and over most of its ontogeny, and to ask questions heretofore impractical. In doing so, they allowed me to address parasitological and ecological issues at scales never before attempted and issues that may have practical implications benefitting a commercially important resource.

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